

Small mammal inventory in the Shipstern Nature Reserve (Corozal District, Belize, Central America), a preliminary assessment

Vincent BERSOT

Muséum d'histoire naturelle, CP 6434, CH-1211 Genève 6, Switzerland.

Small mammal inventory in the Shipstern Nature Reserve (Corozal District, Belize, Central America), a preliminary assessment. - This small mammal inventory was conducted between May and September 2000 in the Shipstern Nature Reserve located at the northeastern limit of Belize in the Corozal District, Central America. In 11840 trap nights, 7 species of non-volant small mammals were captured, including 5 species of myomorph rodents and 2 species of didelphid marsupials. One species, *Ototylomys phyllotis*, accounted for 90.8% of the total captures, and may play a major role in the community structure of mammals in the reserve. The presence of *Peromyscus yucatanicus* in Shipstern Nature Reserve constitutes a first mention for Belize, and suggests that its range is extending more southerly to the limit agreed at present. Observations made on *Sigmodon hispidus* lead to formulate the hypothesis of a morphologically smaller population in the south of Quintana Roo, Mexico, and northern Belize, and further underlines the need for a complete revision of the genus in the Yucatán Peninsula. The sympatric diversity concretely obtained in Shipstern Nature Reserve is certainly underestimated, but nevertheless gives substance to the impression of a rodent community that is clearly affiliated to the partly endemic fauna of the Yucatán Peninsula, Mexico.

Key-words: Belize - Yucatán Peninsula - small mammal inventory - Marmosidae - Didelphidae - Heteromyidae - Muridae.

INTRODUCTION

The information currently available to assess the magnitude and geographic distribution of mammalian diversity in Belize remains incomplete and unevenly representative. Indeed, most collecting has been concentrated in a few historically accessible areas in the Maya Mountains, and further north in the Yucatán Peninsula, and today, very few areas (if any) are characterized by a long history of field work on mammals. Among the most important mammalian surveys, Murie (1935) collected for several weeks in 1931 in the vicinity of Belize City and El Cayo (San Ignacio), British Honduras (today's Belize), on his way to Uaxactun, Petén, Guatemala. In 1939 and 1940, after a brief survey in Jamaica and Haiti, I.T. Sanderson & A. Sanderson spent several months collecting along the coast of British Honduras, from Punta Gorda to the

Bahía de Chetumal, prior to continuing their studies in Quintana Roo, Yucatán, and Chiapas, Mexico – part of their collection was studied by Hershkovitz (1951). Subsequently, additional lists of mammals arose from various research projects. Those include Disney (1968), Dieckman (1973), Kirkpatrick & Cartwright (1975), Burton *et al.* (1987), Rabinowitz & Nottingham (1989), and most recently Caro *et al.* (2001). However, few studies ever focused on the small mammal fauna of Belize. Consequently, methods used to trap marsupials and small rodents often remained adapted to common and generalist species, but proved to be unsuitable to catch specialists and/or rare species. In this context, recent accounts of mammalian diversity in Belize, such as the checklist proposed by McCarthy *et al.* (1998), still probably underestimate the number of small mammal species actually found in the country – this is especially true for the northeastern portion of the country (Corozal District) where studies on the mammalian fauna remain scarce.

In Shipstern Nature Reserve (SNR), as far as can be concluded from the available sources, non-volant small mammals were only briefly surveyed prior to the present study. This was done by Meerman (1993), and Miller *et al.* (1995), in a first attempt to survey the overall mammalian fauna of SNR. Apart from the latter, no other studies on mammals were reported from the reserve, with the exception of a bat inventory carried out by Bärtschi (1998). Nevertheless, other groups of vertebrates, but also invertebrates, were inventoried in SNR. Those include the following checklists: birds, reptiles, amphibians, and some miscellaneous invertebrates (Meerman, 1993); dragonflies and damselflies (Boomsma, 1993); butterflies (Meerman & Boomsma, 1993); and freshwater fishes (Bijleveld, 1990). In addition, beside a checklist of the flora proposed by Meerman (1993), two research projects focusing on the vegetation of SNR were recently carried out by Bijleveld (1998) – structure and floristics – and Sayer (2000) – phenology.

In northern Belize therefore, there is a clear need towards an aggressive programme of short-term mammalian surveys, that are combining the advantage of concreteness – listed species are definitely known to have occurred together at a particular place and time – with the disadvantage of incompleteness. Indeed, although indispensable, a long-term inventory project would inevitably be time-consuming and expensive, now bulldozers and chain saws work faster than field biologists (Voss & Emmons, 1996). In this context, the most important role for this project was to rapidly provide crucial diversity data – maximized by focusing on marsupials and rodents, that is taxa known to respond to ecological or zoogeographic gradients – for future research and conservation objectives implicating the Shipstern Nature Reserve and its surrounding areas. In this respect, the primary objective was to obtain fresh material – voucher specimens that are well preserved, complete, precisely labeled, and documented with exhaustive and informative data – to be subsequently incorporated in the collections of the Natural History Museum, Geneva (MHNG), Switzerland. In turn, the liver was sampled, and saved for DNA preservation, from each of these voucher specimens, so as to constitute a precious tissue collection, completed with ear biopsies sampled from the specimens released in the field. These ear and liver samples were taken for inclusion into the Collection of Preserved Mammalian Tissues (Catzeffis, 1991) held at Montpellier, France, where they are at the disposal of scientists.

Apart from recording the small mammals and preserving their DNA, the other objective of this study was to collect their ectoparasites, and list the endoparasites of their digestive tract – giving priority to the classes Trematoda and Cestoidea, and the phylum Nemata – to be included in the MHNG museum collection. Indeed, obtaining parasites from mammals that are collected during inventories is also time-consuming, and such collections have rarely been made. Parasites and other symbionts are important components of the biology of the host, however, and must be sampled for a complete picture of its ecology and other aspects of its life history. Of course, studies of the systematics and ecological characteristics of hosts and parasites require proper identification of both groups. Now, as far as the ecto- and endoparasites collected in SNR are concerned, this could not be achieved, and deeper analyses will be carried out within the framework of a subsequent study.

STUDY AREA

Previously owned by a British Limited Company, the area was partly managed as a private reserve during the eighties known as the Shipstern Wildlife Preserve. In 1989, it became the property of the International Tropical Conservation Foundation (ITCF), and the name Shipstern Nature Reserve was given. This newly created foundation followed the opening of the tropical butterfly garden Papiliorama of Marin-Neuchâtel in Switzerland, in 1988. Today a major tourist attraction, and further developed as the Papiliorama Swiss Tropical Gardens in Kerzers, Fribourg, it is actively concerned with the conservation of tropical biodiversity through two sister-foundations: the Papiliorama-Nocturama Foundation in Switzerland, and the ITCF in Belize. Thus, among other projects involving the local community, two new protected areas were opened by the ITCF during the last few years: the Xo-Pol area in 1994; and the Sarteneja National Tree Park in 1999. In parallel, the ITCF assisted the Belize Coastal Unit in the creation of the Bacalar Chico National Park & Marine Reserve, in 1996, which is part of the Belizean network of the UNESCO World Heritage Sites. At the same time in SNR, scientific work has been and is being further developed by the ITCF in conjunction with the universities of Bern, Neuchâtel, and Fribourg, Switzerland.

Located at the northeastern limit of Belize in the Corozal District (Figs 1, 2), the Shipstern Nature Reserve covers an area of approximately 9000 hectares (22000 acres). It encompasses part of the Shipstern Lagoon, which is in direct contact with the southern waters of Chetumal Bay, and it also includes the separate surface of Xo-Pol (600 hectares). By land, the only means of access to the area is an all-weather road starting at Orange Walk, and ending at the fishermen village of Sarteneja.

Apart from a coastal plain stretching all along the Belizean coast, the whole area between Belmopan and Corozal (Fig. 1) is covered by lowlands that are further extending northward from Chetumal to Cancún on the eastern side of the Yucatán Peninsula, Mexico. To the southwest, these northern lowlands give way to the Maya Mountain massif, the dominant physical feature in Belize, which is the only area where large upfaulted blocks of intrusive and associated metamorphic sedimentary rocks are preponderant (Hartshorn *et al.*, 1984). Such a substrata with only a thin soil cover means that water is essentially drained on the surface, thus constituting an extensive



FIG. 1

Political map of Central America and northern Belize. SNR, Shipstern Nature Reserve.

system of streams and rivers. By contrast, a small scale karst topography is developed in the northern lowlands covered by tertiary limestones, and the area of SNR is thus characteristic with numerous sinkholes, caves, and natural wells, virtually no stream and river system on the surface, and elevations not exceeding 4-5 m (17 ft).

Rainfall at the reserve was measured over a period of four years, between October 1989 and October 1993 (Meerman & Boomsma, 1993). An average annual rainfall of 1260 mm (49.6 inches) was recorded, with a minimum at 1029 mm (40.5 in.), and a maximum at 1610 mm (63.4 in.) – for comparison, annual rainfall shows a considerable increase from north to south in Belize, averaging 1850 mm (73 in.) at Belize City (Belize District), and 4526 mm (178 in.) at Barranco (Toledo District). Such results suggest that Shipstern Nature Reserve is in one of the driest areas in Belize, with a pronounced dry season – in the year of the present study, the months of

February and March appeared to be exceptionally dry, with no rainfall and 10 mm (0.4 in.) respectively (Sayer, 2000). As a consequence, the water level of the Shipstern Lagoon fluctuates on a yearly cycle, and areas close to the lagoon are temporarily flooded during the wet season.

Indeed, rainfall tends to vary markedly in Belize. It starts with a pronounced dry season between the months of January and May. Then, from June to December, rainfall increases gradually to reach a maximum in September. And some years, this is precisely any time from September to November that the wet season turns to a hurricane season. However, if Belize is frequently facing tropical storms, few hurricanes ever reach the country. And as far as the Shipstern Nature Reserve is concerned, among those that did in the past, only two are known to have caused serious damages. The first one, hurricane Janet, hit Belize in 1955, and greatly affected the northern part of the country. As a result, the villages of Sarteneja and Shipstern (Fig. 2), as well as Corozal Town were completely destroyed, whereas the forests in and around the present reserve were almost entirely flattened and burnt by subsequent fires. Because of this, the vegetation of Shipstern Nature Reserve can be considered as being 47 years old, and most of its vegetation types have not yet reached a structural climax. The second one, hurricane Keith, hit the country during the course of the present study, in early October. And if the reserve still suffered from localized falls of large trees, damages caused directly by the wind remained unextensive in the Corozal District—Keith mostly affected San Pedro (Ambergris Cay) and Cay Caulker, both comprised in the range of islands spreading all along the coast. However, unusual fluctuations of the water level caused by extreme rainfalls and inland accumulation of water carried in by the wind, led to serious floods. As a result, the water depth in the Shipstern lagoon was estimated at 4-6 feet, and the village of Chunox, as well as Orange Walk remained surrounded by floods for weeks.

Temperatures exceeding 40°C (104°F) have already been measured in the country (Walker, 1973). And, it is not uncommon to see the temperatures dropping as low as 10°C (50°F) between the months of November and December, when cold air masses enter the country from the north-east. More commonly, however, mean monthly minima range from 16°C (60.8°F) in winter to 24°C (75.2°F) in summer, and maxima from 28°C (82.4°F) to 33°C (91.4°F), with an annual mean temperature of 26°C (78.8°F) (King *et al.*, 1992).

Despite a long-established timber industry, and a history of successive destructions due to natural phenomena, Belize remains covered by substantial areas of natural vegetation. Nowadays, however, an increased demography in Belize coincides with an increased pressure on the forest areas and on the fauna. Of primary concern is the rapid expansion of cultivated lands in the surroundings of the Shipstern Nature Reserve. Indeed, slash and burn cultivation is more and more common in the vicinity of Xo-Pol, whereas a worrying increase in agricultural activities carried on by Mennonites is observed from Little Belize towards Shipstern Lagoon. In addition, selective logging aimed at species such as Santa Maria (*Callophyllum brasiliense*), Ciricote (*Cordia dodecandra*), and Mahogany (*Swietenia macrophylla*) is expanding throughout the eastern forests of Corozal District, and in particular those around Fireburn which are virtually empty of their large trees.

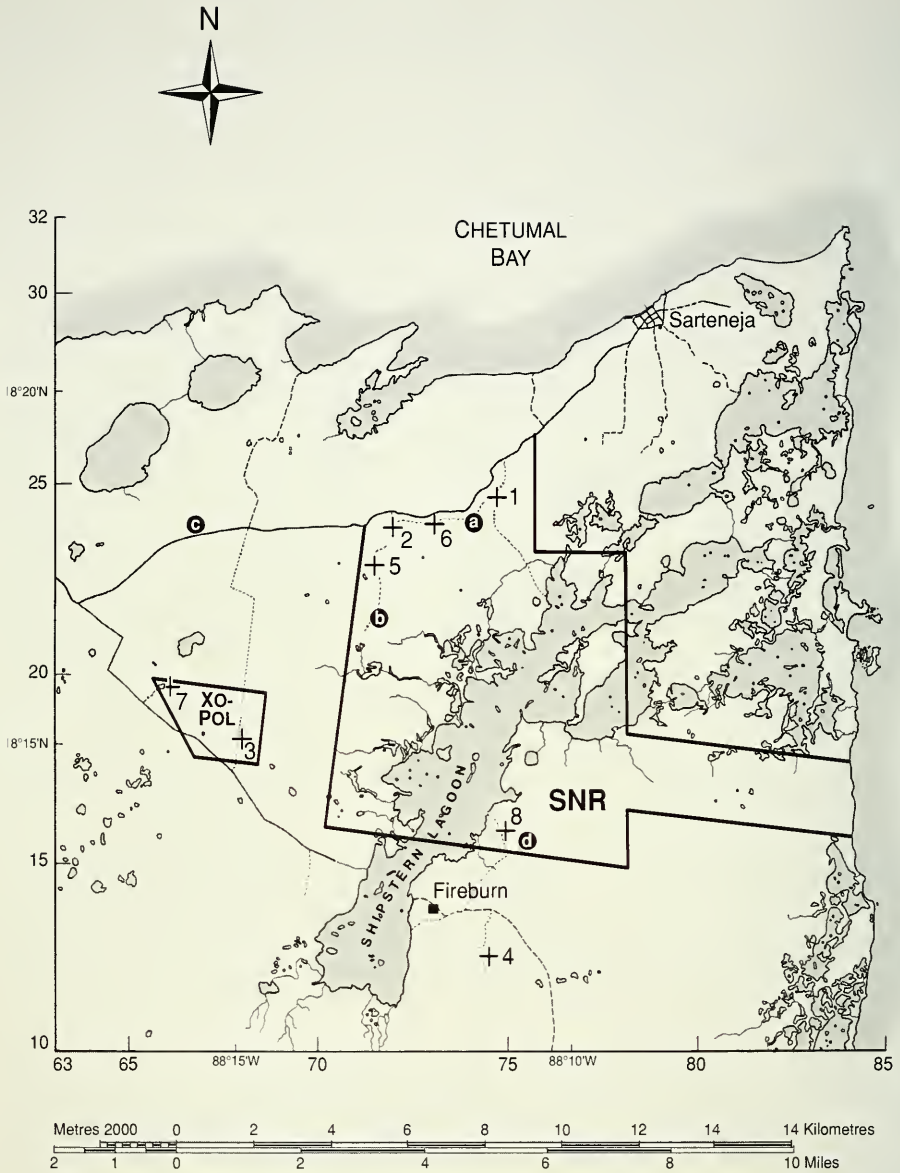


FIG. 2

Map of Shipstern Nature Reserve (SNR). 1-8, trapping sites; a, New Trail; b, Main Trail; c, Main Road; d, Shipstern Old Village. Grid : Universal Transverse Mercator and WGS 84.

In this context, the Shipstern Nature Reserve plays an important role in the country representing one of the very few protected areas in the northern lowlands. Indeed, as far as Belize is concerned, the Yucatecan medium-sized semi-evergreen forests (Table 6) – still well represented over most of the Yucatán Peninsula, this forest

type was probably covering the whole Corozal District before the expansion of sugar cane fields – as well as the very rare Yucatecan medium-sized semi-deciduous forests, are almost exclusively found in and around the reserve. Furthermore, the latter protects the unique patch of Low semi-deciduous *Pseudophoenix s.sargentii* forest distributed on mainland Belize, other patches being localized in the Bacalar Chico National Park & Marine Reserve, and in the Yucatán Peninsula mainly.

With about a third of the surface being occupied by the Shipstern Lagoon, habitats in the reserve appear to be diverse and patchily distributed. Indeed, the lagoon constitutes an intricate system of shallow waters (1-3 feet) bordered by dwarf mangroves and other saline wetlands – listed in the Directory of Neotropical Wetlands (IUCN/IWRB, 1986) – and dotted with numerous small mangrove islands. Besides, so called “forest islands” are randomly distributed in the transitional areas with true forest. And the latter tends to vary considerably in its structural and floristic characteristics, thus creating a complicated mosaic of various forest types – the patches of which are sometimes less than 50 ft wide – that are not always clearly delimited. Aiming for a better understanding of its vegetation, Bijleveld (1998) listed seven main vegetation types within Shipstern Nature Reserve, to which the Cohune forest described by Wright *et al.* (1959) can be added (Table 6).

MATERIALS AND METHODS

Referring to the geographic distribution of the vegetation types listed in table 6, four areas – named New Trail, Main Trail, Xo-Pol, and Shipstern for more convenience – were selected in and around Shipstern Nature Reserve. Chosen on the basis of their accessibility and the presence of ecotones between characteristic habitats, two trapping sites were attributed to different localities within each of these areas. Thus, trapping sites 1/6, 2/5, 3/7, and 4/8, were representative of the New Trail, Main Trail, Xo-Pol, and Shipstern areas respectively (Fig. 2).

Each of the eight trapping sites were identically built by reproducing a standardized trap design (Patton *et al.*, 2000). It consisted of two parallel transects separated by a distance of 500 ft (150 m). Each trapping line was 940 ft (285 m) in length and subdivided into 20 trap stations at 50 ft (15 m) intervals. In turn, four traps were positioned at each trap station, for a total number of 160 traps per trapping site.

One folding Sherman (23 x 7.5 x 7.5 cm) and three folding BTS – Besançon Techniques Services, Besançon, France – mesh (28 x 10.5 x 10.5 cm) live traps were set at each trap station. Traps were placed in the most likely microhabitat within 7 to 17 ft (2-5m) of the station marker. Wherever possible, two BTS mesh live traps were positioned from a height of 4 to 14 ft (1-4 m), whereas the third one remained terrestrial. The Sherman live trap was always set on the ground. For bait, the dried fruit of Guaya trees (*Talisia olivaeformis*) was fixed on the hook of BTS mesh live traps, and coated with peanut butter – no baits were used for Sherman live traps.

All traps were left open for 10 consecutive nights, thus totalling 1600 “trap nights” per locality (Wilson *et al.*, 1996). Eight trapping sessions were scheduled over a 6 month time interval in the year 2000, and effective trapping periods took place at the dates presented in table 3. The last trapping session (site n°8) totalled only 640 trap

nights, having been brutally interrupted under the threat of hurricane Keith. Therefore, trapping effort for all 8 trapping sessions together totalled 11840 trap nights.

First captures of newly encountered species were systematically brought back to the base camp for a first identification based on the external morphology. At the same time, ectoparasites and intestinal endoparasites were sampled along with the liver. After collection of several male and female adults within one species, the specimens captured successively and satisfactorily identified as belonging to the same species were only then released. Standard data – external measurements, weight, sex, age,... – along with an ear sample – a triangular incision of 4-5 mm in the ear pinna – were collected from each individual to be released. The animal was thus marked and recognized if recaptured.

External measurements are expressed as follows (Nagorsen & Peterson, 1980; Catzeflis *et al.*, 1997; Musser *et al.*, 1998): **E**, ear length (distance from the base of the notch of the lower part of the ear to the uppermost margin of the ear); **HF**, hind foot (distance from the end of the heel bone, calcaneum, to the end of the longest toe, exclusive of the claw); **NEB**, nose-ear basis (distance from the tip of the nose to the base of the notch of the lower part of the ear); **NEC**, nose-eye corner (distance from the tip of the nose to the anterior corner of the eye); **SR**, scale rows (number of scale rows in a centimeter section of the tail about one-third from the body); **TL**, total length (straight-line distance from the tip of the nose to the end of the last tail vertebra, exclusive of hair); **TV**, tail vertebrae (distance from the base of the tail to the tip of the last vertebra, exclusive of hair).

At MHNG, the voucher specimens were essentially re-identified by referring to their corresponding skull measurements and cranial characters. The latter data was compared to that found in available literature by first assigning age classes – juvenile, immature, subadult, adult, or old adult (Wilson *et al.*, 1996) – based on tooth eruption and wear to each specimens. Then, whenever a set of skull measurements was not clearly affiliated to one species, distinctive cranial characters were considered as reliable. In addition, the data obtained in the field was finally reexamined, along with the known distribution of the diagnosed species. As a result, the final identification of each specimen was based on the following data: external morphology, external and skull measurements, cranial characters, and distribution.

In murid rodents, skull measurements (Fig. 3) are expressed as follows (Patton *et al.*, 2000; Musser *et al.*, 1998; Voss, 1988): **BB**, braincase breadth; **BBP**, breadth of bony palate; **BIF**, breadth of incisive foramina; **BL**, length of auditory bulla; **BM1**, breadth of first upper molar; **BOL**, basioccipital length; **BR**, breadth of rostrum; **BW**, breadth of auditory bulla; **BZP**, breadth of zygomatic plate; **CBL**, condylobasal length; **CD**, cranial depth; **CIL**, condyloincisive length; **CLM1-3**, crown length of maxillary toothrow; **CLMT**, crown length of mandibular toothrow; **DI**, depth of incisor; **HI**, height of incisor; **IB**, interorbital breadth; **LB**, lambdoidal breadth; **LBP**, length of bony palate; **LD**, length of diastema; **LIF**, length of incisive foramina; **LM**, length of mandible; **MB**, mastoid breadth; **MPFL**, mesopterygoid fossa length; **MPFW**, mesopterygoid fossa width; **NL**, nasal length; **OCB**, occipital condyle breadth; **OL**, orbital length; **ONL**, occipitonasal length; **PL**, palatal length; **PPL**, postpalatal length; **RL**, rostral length; **ZB**, zygomatic breadth.

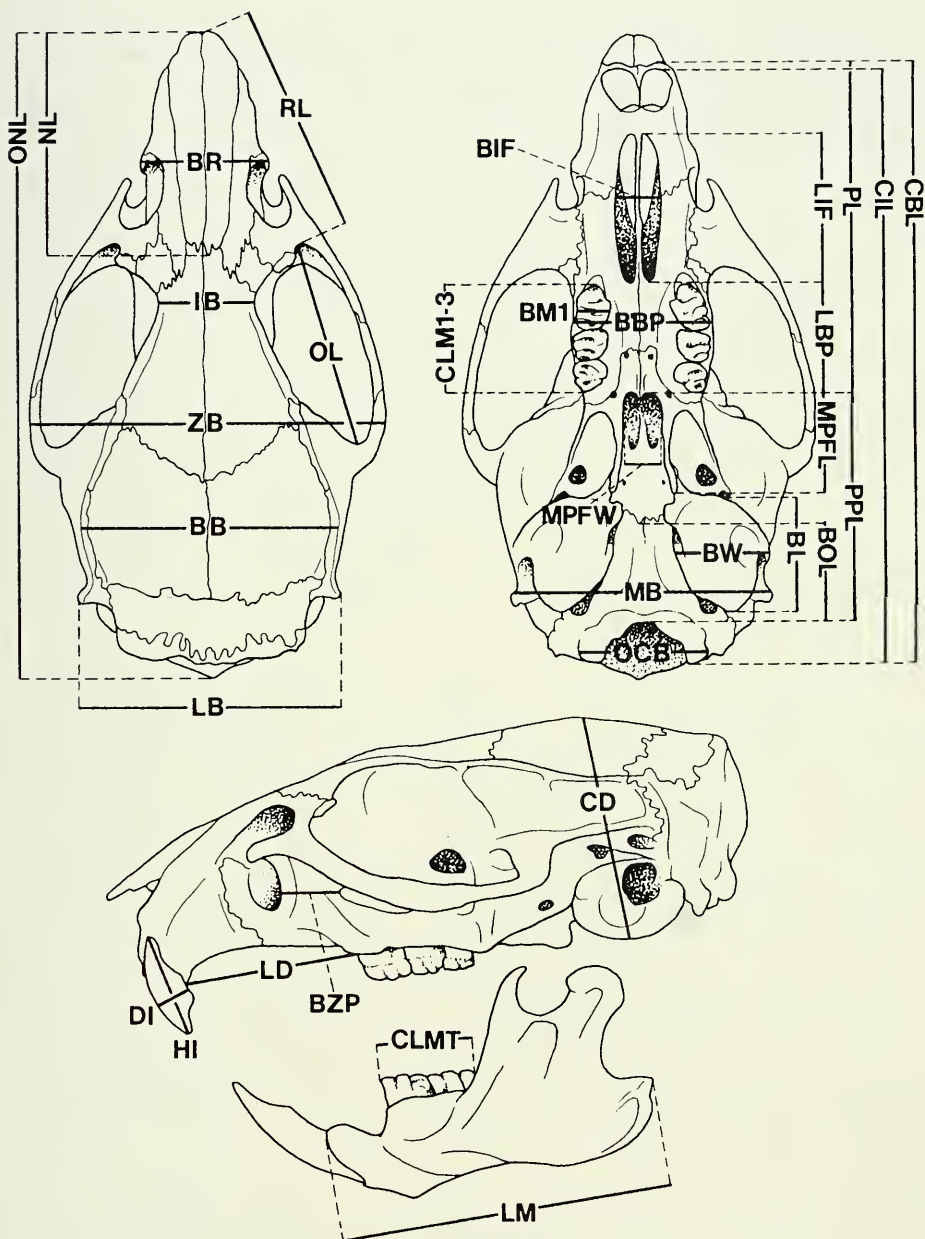


FIG. 3

Rodents, limits of 33 cranial and dental dimensions. Abbreviations are defined in text.

In marsupials, skull measurements (Fig. 4) are expressed as follows (Patton *et al.*, 2000; Gardner, 1973): **BB**, braincase breadth; **BN**, greatest breadth of nasals; **BOL**, basioccipital length; **BRF**, breadth of rostrum across frontals; **BRJ**, breadth of rostrum across jugals; **CBL**, condylobasal length; **CD**, cranial depth; **CLMT**, molar tooththrow length (mandible); **C-M4**, maxillary tooththrow length; **IB**, interorbital breadth; **IOC2**, postorbital constriction; **LM**, length of mandible; **MB**, mastoid breadth; **M1-M4**, molar tooththrow length (maxillary); **NL**, nasal length; **OCB**, occipital condyle breadth; **ONL**, occipitonasal length; **PL**, palatal length; **PPL**, postpalatal length; **PW**, palatal width; **RL**, rostral length; **RW**, rostral width; **ZB**, zygomatic breadth.

A first capture (Table 1) was defined as the first occasion that an individual was trapped and marked (Stallings, 1989). The first capture plus subsequent captures of each specimen were considered total captures. Recapture indices were calculated by dividing total captures by first captures, thus indicating the average number of times an individual of each species was captured. The number of trap nights (Table 3) was calculated by the number of traps multiplied by the number of nights the traps were activated per site (Wilson *et al.*, 1996). The trapping success (Table 3) for a site was the number of total captures of all species divided by the number of trap nights and expressed in percentage. The standard error for each external and cranial measurements (Tables 4, 5) was calculated after Fowler *et al.* (1998).

RESULTS

Capture results by species for the eight trapping sites are presented in table 1. Seven small mammal species were sampled: *Marmosa mexicana* (Merriam, 1897), *Didelphis virginiana* (Kerr, 1792), *Heteromys gaumeri* (Allen & Chapman, 1897), *Otonyctomys hatti* (Anthony, 1932), *Ototylomys phyllotis* (Merriam, 1901), *Peromyscus yucatanicus* (Allen & Chapman, 1897), and *Sigmodon hispidus* (Say & Ord, 1825). Overall, *O.phyllotis* represented 90.8% and 86.6% of the total and first captures respectively. On average, individuals of this species were recaptured at a rate of 1.8 times. Trapping success by trapping site is presented in table 3. A total of 414 captures was obtained in 11840 trap nights, thus yielding an overall trapping success of 3.5%. Table 2 presents for each species the number of total captures per vegetation type (Table 6). However, caution should be taken when comparing the latter results, as the trapping effort is unequal from one vegetation type to another. External and cranial measurements by species presented in tables 4 and 5 combine adult males and females. Here again, attention should be given as the single specimens of *D.virginiana* and *O.hatti* are immature and subadult respectively.

SPECIES ACCOUNTS

The following accounts present the essential observations regarding the morphological description – skull and hindfoot – the local distribution, and the habitat of the 2 species of marsupials and 5 species of rodents captured in Shipstern Nature Reserve. Additional observations of these species are presented in the referred literature. The attribution of a name species to the specimens collected in SNR is also discussed, knowing that few genera of Neotropical rainforest mammals are wholly free of taxonomic problems.

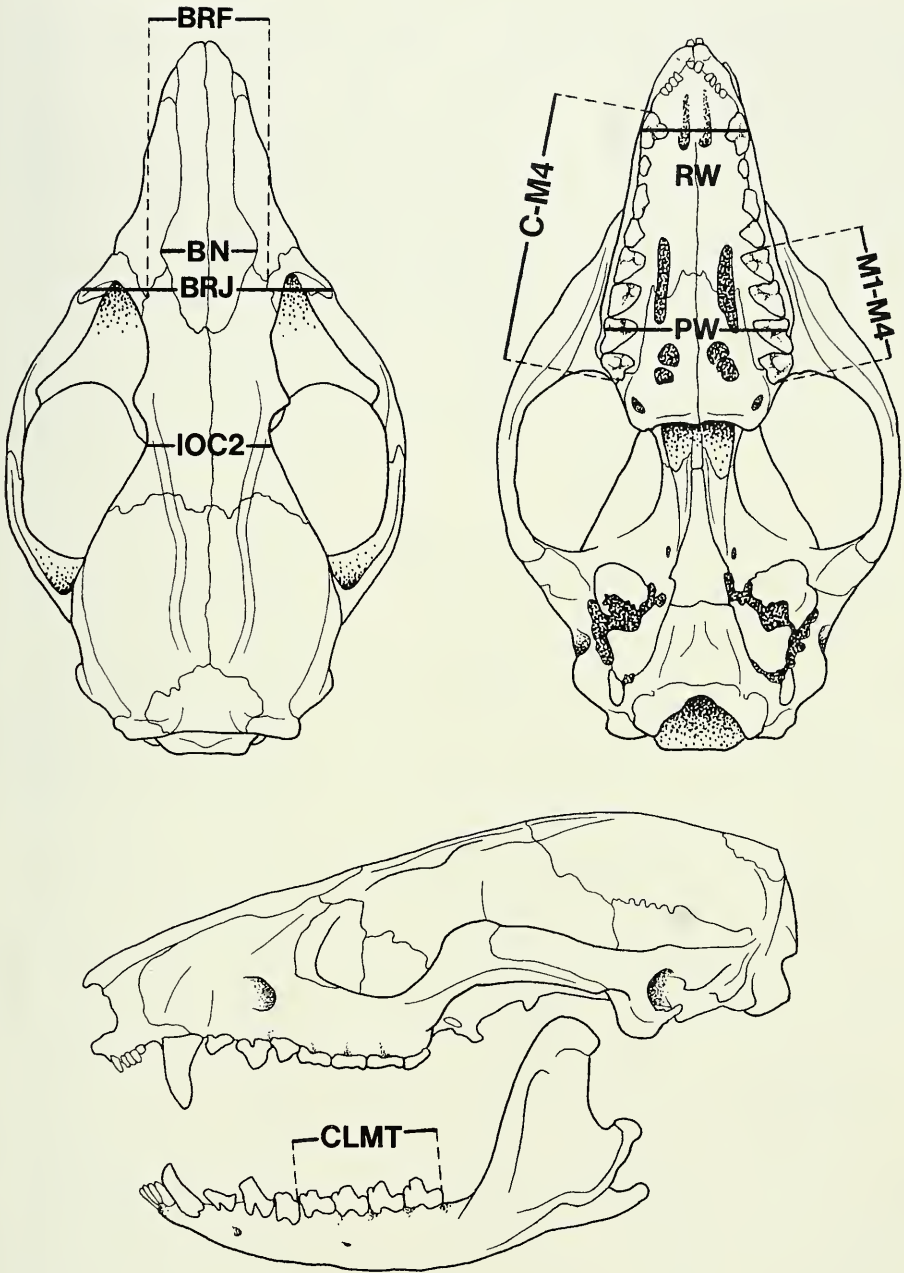


FIG. 4

Marsupials, limits of 9 cranial and dental dimensions. Abbreviations are defined in text. Other measurements, see figure 3.

Family MARMOSIDAE

Marmosa mexicana (Merriam, 1897)

Figs 5, 8

Mexican Mouse Opossum

DESCRIPTION. The cranium is broad and moderately elongate, with a convex dorsal profile (Fig. 5). The rostrum is rather short and broad, concealing the nasolacrimal capsules in dorsal view. The nasals are long and truncate posteriorly, projecting anteriorly beyond the premaxillae to conceal the nasal orifice from dorsal view. The zygomatic arches are stout, convex from the dorsal aspect, convergent anteriorly, and forming a clear elbow-shaped bend in lateral view. The inferior zygomatic root is running on from M4 posteriorly. The interorbital region is broad relative to braincase, without pronounced postorbital constriction. The supraorbital ridges are moderately grooved dorsally, project laterally only slightly, and transform posteriorly into conspicuous parietal ridges on top of braincase. The braincase is narrow, uninflated, with slanting lateral, and nearly vertical rear walls. Occipital ridges are present, but temporal and lambdoidal ridges are not. The auditory bullae are small and moderately rounded, and their anterior margin lies anteriorly to the basisphenoid/basioccipital suture. The basisphenoid is narrow and elongate, contrasting with a short and wide basioccipital. The bony palate is broad, fenestrated, and extends beyond the molar rows posteriorly. The anterior margin of the maxillary/palatine suture lies anteriorly to M2. The incisive foramina are short, inconspicuous, and their posterior margin is level with the posterior face of the upper canines. The teeth are small and number 50. The maxillary toothrows are straight along their labial margins, and convergent anteriorly. The canines are rather short and slender, and PM1 is remarkably smaller than PM2. The dental formula is : i 5/4, c 1/1, p 3/3, and m 4/4. The dentary has a long and stout coronoid process, a well developed condyloid process, a rather delicate angular projection, and a moderately deep and elongate ramus.

Pes has swivelling ankle joints, and opposable hallux (Fig. 8). The plantar surface of pes is unpigmented, devoid of distinctive scalation, naked from heel to tips of the digits, with little fringing hairs along its contour, and with four separate interdigital and two separate carpal pads; the thenar and first interdigital, and the hypothenar and fourth interdigital pads are nearly fused. Dorsal and lateral surfaces of the metatarsal region and digits are a pale cinnamon and naked-looking, sparsely covered with very short white hairs. Digit I is devoid of claw, and claws on digits II to V are short and unpigmented, with inconspicuous tufts of hair at their base.

DISCUSSION. *M. mexicana* is easily confused with *M. robinsoni*. But, whereas *M.m.* is ubiquitous and a typical Central American endemic (McCarthy *et al.*, 1998), *M.r.* was previously known only from Panama, with disjunct populations in southern Belize and Roatán Island in Honduras (Reid, 1997). However, *M.r.* has recently been reported in Guatemala and El Salvador, so that it may be present throughout Central America, and specimens may have been confused with *M.m.*. A reappraisal of all specimens of the two species in Central America is therefore needed to determine their exact distribution.

On the basis of external characters, *M.m.* and *M.r.* are hardly distinguishable, although *M.r.* is usually larger, with a longer and slightly woolly fur (Reid, 1997). Thus,

these species are best distinguished by skull characters when adult. In the case of VB054 (MHNG n°1812.007), external and cranial measurements (Tables 4, 5) tally perfectly with those of *M.m.* in Alonso-Mejía & Medellín (1992), but are rather at the bottom of the ranges given for *M.r.* in O'Connell (1983). Furthermore, it is clearly characterized by its supraorbital ridges that are moderately grooved dorsally, and project laterally only slightly (Alonso-Mejía & Medellín, 1992), and its postorbital constriction that is not as pronounced as in *M.r.* (O'Connell, 1983).

Serious conclusions on habitat and local distribution cannot be drawn from a single capture (Table 1). Nevertheless, apart from the strong morphological adaptations towards arboreality observed in VB054, the habitat description in Reid (1997) leads to infer that *M.m.* is probably ubiquitous in the forests of Shipstern Nature Reserve.

Family DIDELPHIDAE

Didelphis virginiana (Kerr, 1792)

Figs 5, 8

Virginia Opossum

DESCRIPTION. The cranium is elongate and broad, with a convex dorsal profile (Fig. 5). The rostrum is long and broad, concealing the nasolacrimal capsules in dorsal view. The nasals are long, narrow, and truncate posteriorly, revealing the nasal orifice in dorsal view. The lateralmost extent of each nasal, where intercepted by the maxillo-frontal suture, is aligned from the point where the same suture meets the lacrimal. The lacrimal recedes from the outer margin of the jugal before terminating in an acute point on the superior zygomatic root. The zygomatic arches are stout, convex from the dorsal aspect, and convergent anteriorly. The inferior zygomatic root is running on from M2 posteriorly; M3 is barely erupting. The dorsal extension of the palatine bones that make up part of the inner wall of the orbits is broad. The interorbital region is broad relative to braincase, without pronounced postorbital constriction. The supraorbital ridges are unextensive, moderately grooved dorsally, project laterally only slightly, and transform posteriorly into conspicuous but short and convergent parietal ridges on top of braincase. The braincase is narrow, uninflated, with slanting lateral, and nearly vertical rear walls. Occipital ridges are present, but temporal and lambdoidal ridges are not. The auditory bullae are remarkably small and barely rounded, and their anterior margin lies slightly anteriorly to the basisphenoid/basioccipital suture. The basisphenoid is narrow and rather elongate, contrasting with a short and wide basioccipital. The bony palate is broad, fenestrated, and extends beyond the molar rows posteriorly. The anterior margin of the maxillary/palatine suture lies slightly posteriorly to the margin between M1 and M2. M4 and PM3 are absent, whereas M3 and m4 are erupting. The incisive foramina are short, inconspicuous, and their posterior margin is level with the anterior face of the upper canines. The teeth are fairly broad and number 44. The maxillary toothrows are straight along their labial margins, and convergent anteriorly. The canines are rather short and stout, and PM1 is remarkably smaller than PM2. The dental formula is: $i\ 5/4$, $c\ 1/1$, $p\ 2/2$, and $m\ 3/4$. The dentary has a long and broad coronoid process, a well developed condyloid process, a small but rather stout angular projection, and a deep and elongate ramus.

Pes has swivelling ankle joints, and opposable hallux (Fig. 8). The plantar surface of pes is dark brown, with distinctive scalation, naked from heel to tips of the digits, with little fringing hairs along its contour, and with four separate interdigital and one carpal pads; the hypothenar and fourth interdigital pads are fused, and the thenar and first interdigital pads are nearly so. Dorsal and lateral surfaces of the metatarsal region and digits are blackish and sparsely covered with short black hairs. Digit I is devoid of claw, and claws on digits II to V are relatively long and unpigmented, with tufts of black hair at their base.

DISCUSSION. *D. virginiana* may be difficult to distinguish with certainty from *D. marsupialis* by sight. Also, both species are ubiquitous in Central America – *D. m.* extends from NE Argentina, Bolivia, and Peru in South America to northern Mexico (Reid, 1997), whereas *D. v.*, which is thought to have arisen from *D. m.* (Gardner, 1973), is not found any further than NW Costa Rica, but extends northerly to southern Canada – and are expected to be sympatric in Shipstern Nature Reserve.

Perhaps the most distinctive and easily observed external character separating *D. v.* and *D. m.* is the hair color of the cheek region (Gardner, 1973): it is pure white in *D. v.*, and clearly set off from the rest of the head by the darker color of the sides and neck behind, and by a dark band extending from the ear through the eye above. Also, the extent of the black pigmented basal portion of the tail ranges from half to all black in *D. v.* (Reid, 1997), whereas it tends to be less in *D. m.*, a criterion however considered as too variable for broad application by Gardner (1973). Additional characters observed in *D. v.*, such as long white mystacial and genal whiskers, and more evenly distributed guard hairs over the dorsum, can be useful to separate *D. v.* from *D. m.*, but are still not determining in some cases. Among others, the single specimen captured in this study (VB062, MHNG n°1812.008) is assigned to the age class 2 (Gardner, 1973), and is probably too young to be distinguished with certainty. For the same reason, the external and cranial measurements of VB062 (Tables 4, 5) are not comparable with those given for *D. v.* in McManus (1974), Gardner (1973), and Goodwin (1969). Nevertheless, *D. v.* and *D. m.* can be separated by skull characters that are independent of age classes (Gardner, 1973). Thus, VB062 is clearly characterized by its bone configuration in the naso-lacrimal and lacrimo-jugal regions, and on the inner wall of the orbit.

Just as in the case of VB054, the clear morphological adaptations observed in VB062 confirm that it is highly scansorial. Furthermore, the habitat description in Reid (1997), and McManus (1974), leads to infer that *D. v.* is also ubiquitous in the forests of SNR.

Family HETEROMYIDAE

Heteromys gaumeri (Allen & Chapman, 1897)

Figs 6, 8

Gaumer's Spiny Pocket Mouse

DESCRIPTION. The cranium is elongate and rather slender, with a convex dorsal profile (Fig. 6). The rostrum is long and broad, concealing the nasolacrimal capsules in dorsal view. The nasals are long with slightly convergent outer margins posteriorly, and they project anteriorly beyond the premaxillae to conceal the nasal orifice from

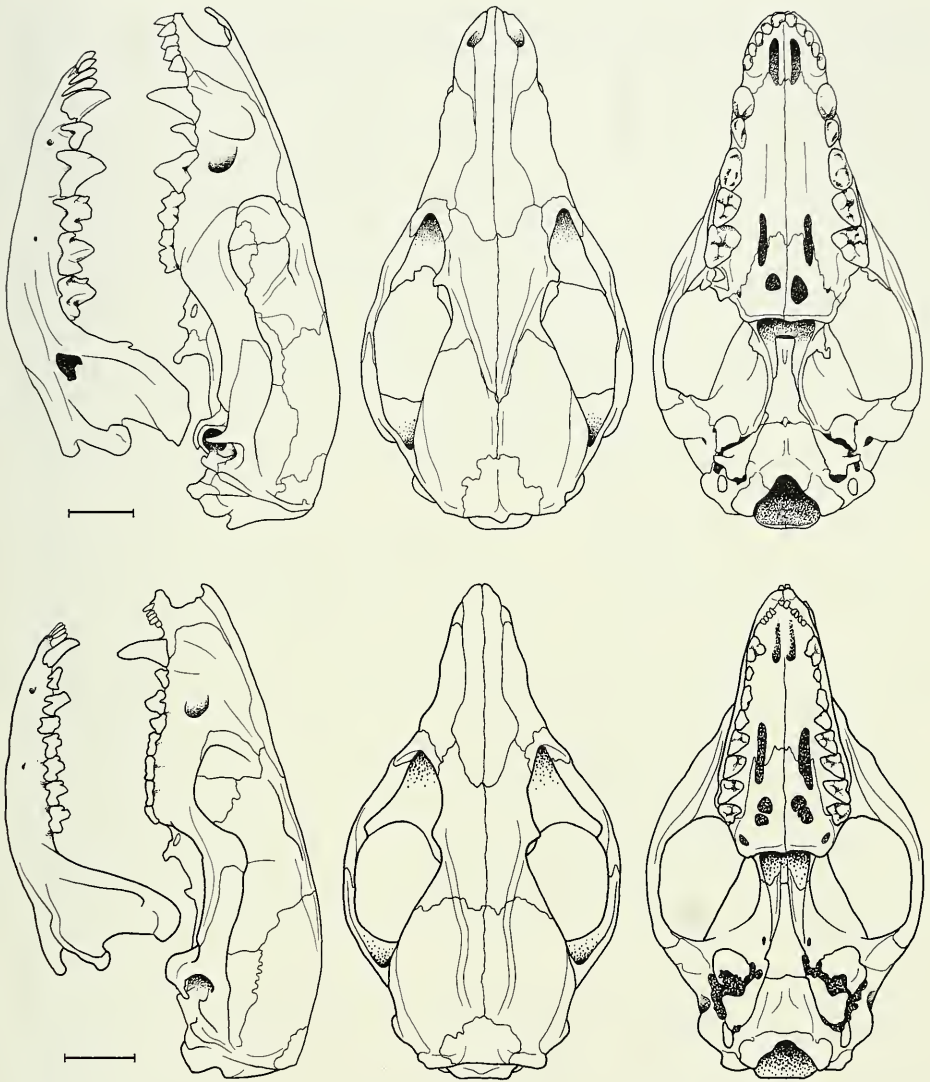


FIG. 5

Top, *Didelphis virginiana* (VB062/MHNG n°1812.008); **bottom,** *Marmosa mexicana* (VB054/MHNG n°1812.007). Dorsal, ventral, and lateral view of cranium and lateral view of left dentary. Scale bars: 5 (*M.m.*) and 7 (*D.v.*) mm.

dorsal view. The zygomatic arches are slender, only slightly convex from the dorsal aspect, and convergent anteriorly. The interorbital region is remarkably broad relative to braincase. Supraorbital shelves accentuate the dorsolateral margins of the interorbit and transform posteriorly into low temporal ridges extending to inconspicuous lamb-

doidal ridges. The supraorbital ridges are moderately grooved dorsally. Occipital ridges are present, and the supraoccipital crest is angular but barely visible in dorsal view. The braincase is moderately inflated but not globose, with nearly vertical lateral and rear walls. The auditory bullae are moderately large and not clearly rounded; their anterior margin lies anteriorly to the basisphenoid/basioccipital suture. The basisphenoid is narrow and short, contrasting with an elongate and moderately wide basioccipital. The bony palate is narrow, without fenestration, and extends beyond the molar rows posteriorly. The anterior margin of the maxillary/palatines suture is level with M2. The incisive foramina are very short and inconspicuous; the premaxillary-maxillary suture joins their posterior margin. The teeth number 20. The molar toothrows are straight along their labial margins, and convergent anteriorly. Incisors are moderately large with smooth orangish enamel faces; in lateral profile, the uppers curve back toward the molar rows, an opisthodont configuration. The dental formula is : i 1/1, c 0/0, p 1/1, and m 3/3. The dentary has a short coronoid process, a rather long and stout condyloid process, a well developed angular projection and a deep but short ramus; the capsular process is visible.

The plantar surface of pes is unpigmented around the interdigital pads and on digits, and is otherwise dark brown; it has four separate interdigital and two separate carpal pads, with distinctive scalation (Fig. 8); it is thinly covered with short dark brown or reddish hairs from heel to thenar and hypothenar pads, with little fringing hairs along its contour. Dorsal and lateral surfaces of the metatarsal region and digits are whitish, and thinly covered with short white hairs. The three middle digits are much longer than the outer two, and interdigital webbing is present between digits II, III, and IV. The claw on digit II is enlarged. Claws are otherwise short and unpigmented, with inconspicuous tufts of hair at their base.

DISCUSSION. *H. gaumeri* is endemic to the Yucatán Peninsula, and its southern range extends no further than N Belize and N Guatemala (Reid, 1997), where it is likely to be found in sympatry with *H. desmarestianus*—although a typical Central American endemic (McCarthy *et al.*, 1998) seemingly absent from the state of Yucatán, Mexico, *H.d.* has been reported to the west of Chetumal, Quintana Roo, Mexico (Jones *et al.*, 1974).

However, *H.g.* differs from all other species of the genus *Heteromys* by the presence of hair on the posterior portion of the sole of the hind foot (Schmidt *et al.*, 1989). Also, whereas very few skull characters are known to separate them, *H.g.* is distinguished from *H.d.* by a discontinuous pelage coloration between the outer surfaces of front legs and dorsum (Reid, 1997), a relatively well haired tail with a conspicuous terminal tuft, and by averaging smaller in most external and cranial measurements. Thus, VB017 (MHNG n°1811.098), VB021 (MHNG n°1811.100), and VB022 (MHNG n°1812.001) tally perfectly with the external and cranial measurements (Tables 4, 5) of *H.g.* in Schmidt *et al.* (1989), and Jones *et al.* (1974), but are below those given for *H.d.* in Rogers & Schmidt (1982), and Goodwin (1969).

All specimens of *H.g.* were caught on the ground, and ran away on the ground, sometimes directly into a near cavity, when released. Besides, no morphological adaptations towards arboreality were observed from sampled specimens, thus suggesting that *H.g.* is strongly terrestrial. Furthermore, the fact that *H.g.* was captured in all sites

except n°1 (Table 1), and in all forest habitats (Table 2), leads to infer that it is ubiquitous in the forests of Shipstern Nature Reserve, and probably absent from exposed areas covered by vegetation types 6 and 7.

Family MURIDAE

Otonyctomys hattii (Anthony, 1932)

Figs 6, 8

Yucatan Vesper Mouse

DESCRIPTION. The cranium is short and rather angular, with a convex dorsal profile (Fig. 6). The rostrum is short and narrow, not concealing the nasolacrimal capsules in dorsal view. The nasals are short, and project anteriorly beyond the premaxillae to conceal the nasal orifice from dorsal view. The zygomatic arches are slender, nearly parallel from the dorsal aspect, strongly convergent anteriorly, and forming downward a pronounced arc-shaped bend in lateral view. The interorbital region is narrow relative to braincase. Supraorbital shelves accentuate the dorsolateral margins of the interorbit and transform posteriorly into temporal ridges extending to conspicuous lambdoidal ridges. The supraorbital ridges are moderately grooved dorsally. Occipital ridges are present, and the supraoccipital crest is rounded but barely visible in dorsal view. The braincase is well inflated but not globose, with nearly vertical lateral and rear walls. The auditory bullae are greatly enlarged and rounded, and their anterior margin lies anteriorly to the basisphenoid/basioccipital suture. Both the basisphenoid and the basioccipital are narrow and elongate. The bony palate is moderately narrow, without fenestration, and does not extend beyond the molar rows posteriorly. The anterior margin of the maxillary/palatines suture is level with the margin between M1 and M2. The incisive foramina are rather long and conspicuous, and their posterior margin lies slightly posteriorly to the anterior margin of the orbits. The teeth number 16. The molar toothrows are straight along their labial margins, and parallel. Incisors are moderately large with smooth orangish enamel faces; in lateral profile, the uppers curve back toward the molar rows, an opisthodont configuration. The dental formula is: i 1/1, c 0/0, p 0/0, and m 3/3. The dentary has a short coronoid process, a very long and stout condyloid process, a well developed angular projection, and a rather deep but short ramus; the capsular process is barely visible.

Pes has moderately swivelling ankle joints, but no opposable hallux (Fig. 8). The plantar surface of pes is unpigmented on digits and otherwise purplish, devoid of distinctive scalation, naked from heel to tips of the digits, with little fringing hairs along its contour, and with four separate interdigital and two separate carpal pads. Dorsal and lateral surfaces of the metatarsal region and digits are pale brown and naked-looking, thinly covered with short white hairs. Claws are short and unpigmented, with a tuft of white hair at their base.

DISCUSSION. Just as *H. gaumeri*, *O. hattii* is endemic to the Yucatán Peninsula, and its southern range extends no further than N Belize and N Guatemala (Reid, 1997; Peterson, 1965). Consequently, although *O. h.* may be confused with *Nyctomys sumichrasti*, their respective ranges are not overlapping – *N. s.* is a typical Central American endemic (McCarthy *et al.*, 1998) seemingly absent from the Yucatán Peninsula, Mexico, apart from southern Belize (Jones *et al.*, 1974) – and they have never been reported as sympatric as yet.

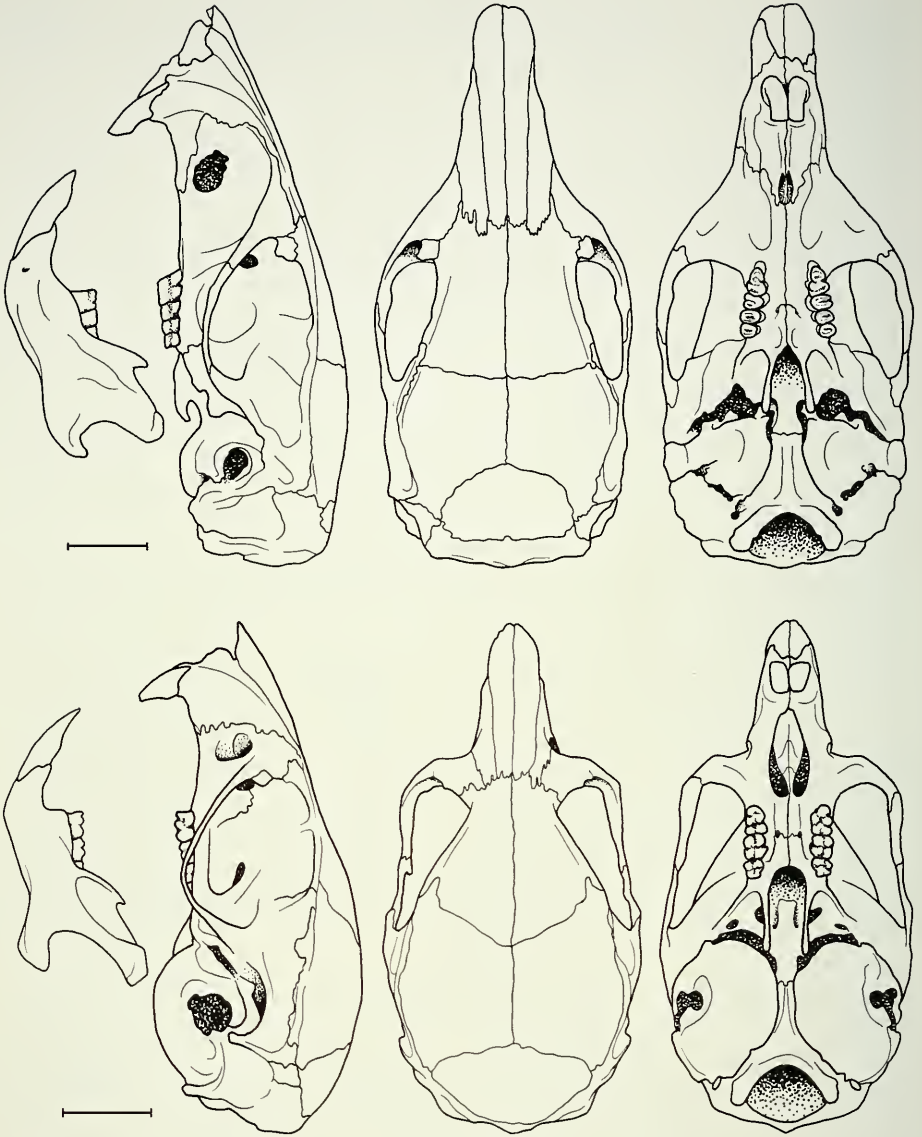


FIG. 6

Top. *Heteromys gaumeri* (VB017/MHNG n°1811.098); **bottom.** *Otonyctomys hatti* (VB182/MHNG n°1812.009). Dorsal, ventral, and lateral view of cranium and lateral view of left dentary. Scale bars: 5 mm.

The single specimen captured in this study (VB182, MHNG n°1812.009) is assigned to the age class II (Genoways & Jones, 1972), and is probably too young to be distinguished with certainty, on the basis of external characters. However, even

knowing that very few skull characters separate *O.h.* from *N.s.*, the skull of VB182 is easily characterized by its greatly enlarged auditory bullae, which are more than twice as large as those of *N.s.* (Peterson, 1965).

VB182 was found to have a remarkable ability to climb on all surfaces of its mesh wire trap. Also, the morphology of its hindfeet with moderately swivelling ankle joints leads to infer that it is scansorial. Besides, by referring to the habitat description in Reid (1997), *O.h.* is likely to be ubiquitous, although rare, in the forests of SNR.

Ototylomys phyllotis (Merriam, 1901)

Figs 7, 8

Big-eared Climbing Rat

DESCRIPTION. The cranium is elongate and rather angular, with a flattened dorsal profile, gently convex over braincase (Fig. 7). The rostrum is long and narrow, not concealing the nasolacrimal capsules in dorsal view. The nasals are rather long and terminate in a rounded angle anteriorly, projecting beyond the premaxillae to conceal the nasal orifice from dorsal view. The zygomatic arches are stout, fairly angular from the dorsal aspect, and strongly convergent anteriorly. The interorbital region is rather broad relative to braincase. Supraorbital shelves accentuate the dorsolateral margins of the interorbit and transform posteriorly into low temporal ridges extending to prominent lambdoidal ridges. The supraorbital ridges are moderately grooved dorsally. Occipital ridges are present, and the supraoccipital crest is clearly angular in dorsal view. The braincase is boxlike, with nearly vertical lateral and rear walls. The auditory bullae are large and rounded, and their anterior margin lies anteriorly to the basisphenoid/basioccipital suture. Both the basisphenoid and the basioccipital are moderately wide and elongate. The bony palate is moderately narrow, without fenestration, and does not extend beyond the molar rows posteriorly. The anterior margin of the maxillary/palatines suture is level with M2. The incisive foramina are long, broad, conspicuous, and their posterior margin lies slightly posteriorly to the anterior margin of M1. The teeth number 16. The molar toothrows are straight along their labial margins, and parallel. Incisors are moderately large with smooth orangish enamel faces; in lateral profile, the uppers curve back toward the molar rows, an opisthodont configuration. The dental formula is: i 1/1, c 0/0, p 0/0, and m 3/3. The dentary has a short coronoid process, a long and stout condyloid process, a broad and well developed angular process, and a moderately deep and short ramus; the capsular process is barely visible.

The plantar surface of pes is unpigmented on digits and pads, and otherwise purplish, devoid of distinctive scalation, naked from heel to tips of the digits, with little fringing hairs along its contour, and with four separate interdigital and two separate carpal pads (Fig. 8). Dorsal and lateral surfaces of the metatarsal region and digits are greyish white, and thinly covered with short white hairs. Claws are short and unpigmented, with a tuft of white hair at their base.

DISCUSSION. *O. phyllotis* is a typical Central American endemic (McCarthy *et al.*, 1998), ubiquitous in the Yucatán Peninsula.

Whereas few skull characters are distinctly separating *O.p.* from a species such as *Tylomys nudicaudus* – also a Central American endemic, seemingly absent from the states of Campeche, Yucatán, and Quintana Roo, Mexico (Reid, 1997; Jones *et al.*,

1974), but likely to be sympatric with *O.p.* throughout Belize – on the basis of external characters, it can hardly be confused with any other species. Indeed, *O.p.* is characterized by a conspicuous patch of white fur at the ear basis. Also, if both species have a shiny, naked-looking, and broadly scaled tail, its distal half is white or yellow pigmented in *T.n.* (Lawlor, 1982). Besides, *O.p.* averages smaller in most external and cranial measurements. In the case of VB001 (MHNG n°1811.089), VB002 (MHNG n°1811.090), VB004 (MHNG n°1811.091), VB005 (MHNG n°1811.092), VB063 (MHNG n°1811.094), VB105 (MHNG n°1811.096), VB121 (MHNG n°1811.097), and VB128 (MHNG n°1812.061), however, the latter are rather at the bottom, or even below (Tables 4, 5), the measurements given for *O.p.* in Lawlor (1982). Nevertheless, the same author (1969) reported that *O.p.* is characterized by considerable local and geographic variation in size and pelage coloration – it varies gradually from small and dusky brown in the lowlands of the Yucatán Peninsula, to large and dark greyish-brown in Costa Rica, and in the highlands of Chiapas and Guatemala.

Specimens of *O.p.* were caught at all levels from the ground to a height exceeding three meters. Also, when released, most of them ran away on the ground, sometimes directly into a near cavity, whereas a fraction of them climbed on the surrounding vegetation before returning to the ground. Such observations were also recorded by Lackey (1989), and suggest that *O.p.* is terrestrial – numerous dens were observed in the ground – but also very common in the vegetation composing the forest understory. Besides, the fact that *O.p.* was captured in all sites (Table 1), and in all forest habitats (Table 2), leads to infer that it is ubiquitous in the forests of SNR, and probably absent from exposed areas covered by vegetation type 7. Furthermore, regarding the percentage of total captures recorded for *O.p.* (Table 1), and the frequent observations of predators around the traps, the big-eared climbing rat is certainly important in the diets of many sympatric vertebrate carnivores in SNR.

Peromyscus yucatanicus (Allen & Chapman, 1897)

Figs 7, 8

Yucatan Deer Mouse

DESCRIPTION. The cranium is elongate and rather slender, with a convex dorsal profile (Fig. 7). The rostrum is long and narrow, not concealing the nasolacrimal capsules in dorsal view. The nasals are long and terminate in a rounded angle anteriorly, projecting beyond the premaxillae to conceal the nasal orifice from dorsal view. The zygomatic arches are slender, parallel from the dorsal aspect, strongly convergent anteriorly, and forming downward a pronounced arc-shaped bend in lateral view. The interorbital region is narrow relative to braincase. Supraorbital shelves accentuate the dorsolateral margins of the interorbit and transform posteriorly into barely visible low temporal ridges extending to inconspicuous lambdoidal ridges. The supraorbital ridges are moderately grooved dorsally. Occipital ridges are absent, and the supraoccipital at its margin with the interparietal is smooth in dorsal view. The braincase is inflated but not globose, with nearly vertical lateral and rear walls. The auditory bullae are moderately large and not clearly rounded; their anterior margin lies anteriorly to the basisphenoid/basioccipital suture. Both the basisphenoid and the basioccipital are moderately wide and elongate. The bony palate is rather broad, without fenestration, and does not extend beyond the molar rows posteriorly. The anterior margin of the

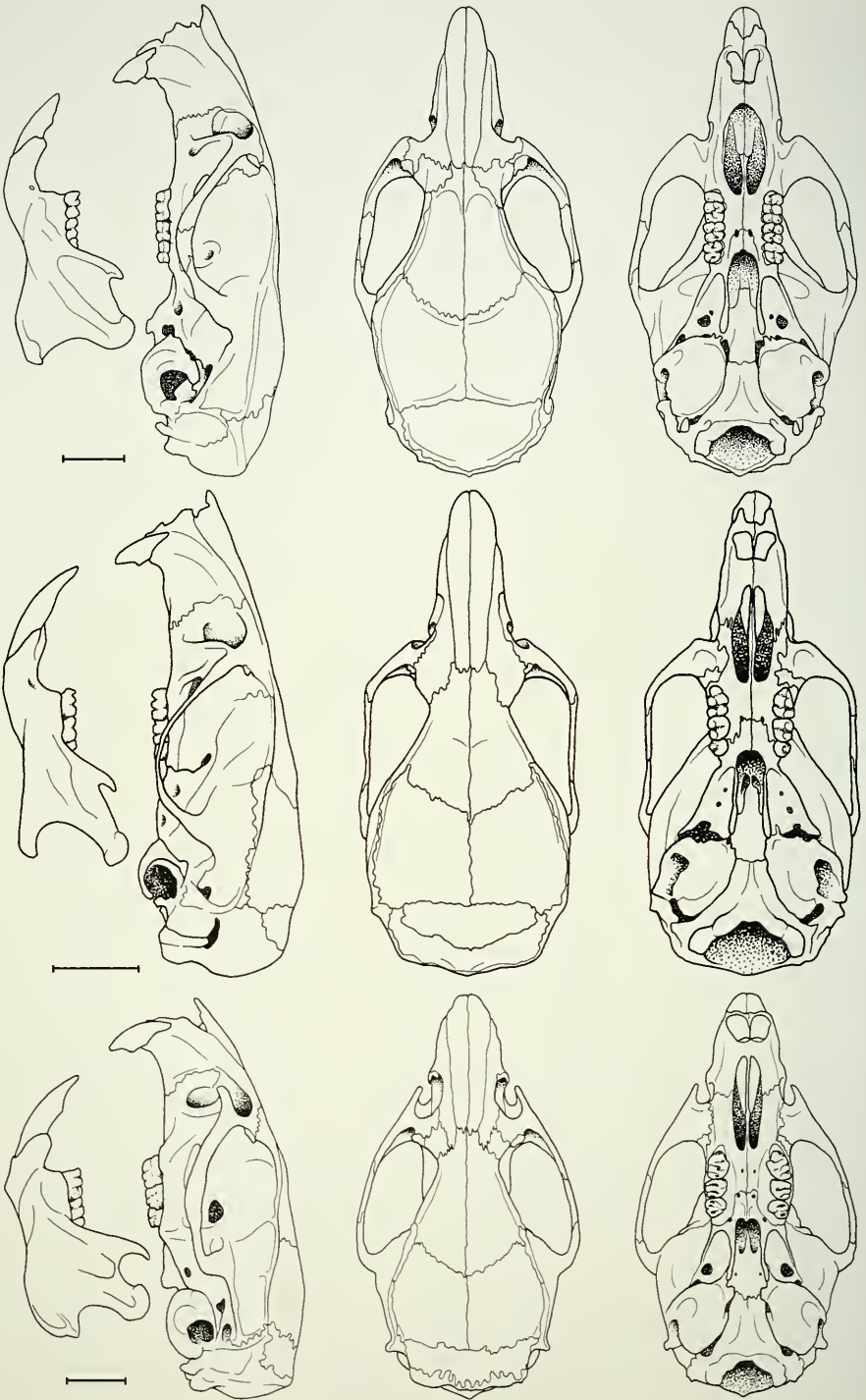
maxillary/palatines suture is level with the margin between M1 and M2. The incisive foramina are long and conspicuous, and their posterior margin is level with the anterior margin of the orbits. The teeth number 16. The molar toothrows are only slightly convex along their labial margins, and slightly convergent posteriorly. Incisors are moderately large with smooth orangish enamel faces; in lateral profile, the uppers curve back toward the molar rows, an opisthodont configuration. The dental formula is : i 1/1, c 0/0, p 0/0, and m 3/3. The dentary has a falciform coronoid process, a long and stout condyloid process, a well developed angular process, and a moderately deep and short ramus; the capsular process is barely visible.

The plantar surface of pes is greyish-brown, devoid of distinctive scalation, thinly covered with short black hairs on the heel, with little fringing hairs along its contour, and with four separate interdigital and two separate carpal pads (Fig. 8). Dorsal and lateral surfaces of the metatarsal region and digits are white, thinly covered with short white hairs. Claws are short and unpigmented, with a tuft of white hair at their base.

DISCUSSION. *P.yucatanicus* is easily confused with *P.mexicanus*. Nevertheless, *P.m.* is a typical Central American endemic seemingly absent from the Yucatán Peninsula, Mexico, apart from southern Belize (McCarthy *et al.*, 1998). Whereas *P.y.* is endemic to the Yucatán Peninsula, and its present southern range extends no further than in the southern part of the states of Campeche and Quintana Roo, Mexico (Reid, 1997). Consequently, their respective ranges are not overlapping, and *P.y.* is considered as allopatric from *P.m.* (Young & Jones, 1983). However, Huckaby (1980) reported that the southern limits of the range of *P.y.* are not clearly known, which is confirmed by the present study. Indeed, the presence of *P.y.* in Shipstern Nature Reserve constitutes a first mention for Belize (McCarthy *et al.*, 1998), and suggests that its range is extending more southerly to the limit agreed at present.

On the basis of external characters, *P.y.* and *P.m.* are hardly distinguishable; *P.y.* differs in being smaller, both externally and cranially (Young & Jones, 1983). In the case of VB225 (MHNG n°1812.010), the external and cranial measurements (Tables 4, 5) tally perfectly with those of *P.y.* in Lawlor (1965), Huckaby (1980), and Lackey (1976), but are below the ranges given for *P.m.* in Huckaby (1980), and Goodwin (1969). Nevertheless, it is best distinguished from *P.m.* by the accessory ridges of its upper and lower molars that are well-developed and fused with the labial styles (Lawlor, 1965; Hooper, 1957).

Although serious conclusions cannot be drawn from two isolate captures, the fact that VB089 and VB225 were captured on the ground and at a height of 2 ft respectively, and that no morphological adaptations towards arboreality were observed, suggest that it is mainly terrestrial, with a moderate ability to climb on the low vegetation composing the understory. Furthermore, the habitat description in Reid (1997) leads to infer that *P.y.* is probably ubiquitous in the forests of Shipstern Nature Reserve, although it was only recorded from the Shipstern area (Fig. 2).



Sigmodon hispidus (Say & Ord, 1825)

Figs 7, 8

Hispid Cotton Rat

DESCRIPTION. The cranium is short and rather broad, with a moderately convex dorsal profile (Fig. 7). The rostrum is short and broad, but not concealing the deeply excavated nasolacrimal capsules in dorsal view. The nasals are short and terminate in a rounded angle anteriorly, projecting beyond the premaxillae to conceal the nasal orifice from dorsal view. The zygomatic arches are stout, convex from the dorsal aspect, and convergent anteriorly. The interorbital region is rather narrow relative to braincase. Supraorbital shelves accentuate the dorsolateral margins of the interorbit and transform posteriorly into low temporal ridges extending to conspicuous lambdoidal ridges. The supraorbital ridges are grooved dorsally. Occipital ridges are present, and in average 3.1 mm distant from temporal ridges. The supraoccipital crest is angular in dorsal view, but also when viewed posteriorly. The braincase is only slightly inflated, with nearly vertical lateral and rear walls. The auditory bullae are moderately large and rounded; their anterior margin lies anteriorly to the basisphenoid/basioccipital suture. The basisphenoid is short, contrasting with a wide and rather elongate basioccipital. The diameter of the foramen ovale is less than three-quarters the diameter of M3. The bony palate is fairly broad, without fenestration, and with a well-developed median crest extending beyond the molar rows posteriorly (spinous process). The anterior margin of the maxillary/palatines suture is level with M2. The spinous anterodorsal process of the zygomatic plate is blunt, but clearly visible. The incisive foramina are long, narrow, conspicuous, and their posterior margin lies slightly posteriorly to the anterior margin of the orbits. The teeth number 16. The molar toothrows are convex along their labial margins, and slightly convergent anteriorly. Incisors are large with ungrooved orangish enamel faces; in lateral profile, the uppers curve back toward the molar rows, an opisthodont configuration. The dental formula is: $i\ 1/1$, $c\ 0/0$, $p\ 0/0$, and $m\ 3/3$. The dentary has a falciform coronoid process, a long and stout condyloid process, a broad and well developed angular process, and a deep and short ramus; the capsular process is clearly visible.

The plantar surface of pes is dark grey, with a distinctive scalation, naked from heel to tips of the digits, with conspicuous fringing hairs along its contour, and with four separate interdigital and two separate carpal pads (Fig. 8). Dorsal and lateral surfaces of the metatarsal region and digits are grey, and thinly covered with short orangish or silvery hairs. The three middle digits are much longer than the outer two, and have enlarged claws. Claws are otherwise greyish, with a conspicuous tuft of silvery hair at their base.

DISCUSSION. The relationships among the seven valid species of the genus *Sigmodon* that are currently recognized in North and Central America have long been the subject of controversy, and the genetic integrity of *S. hispidus* cannot be assumed as yet (Elder & Lee, 1985; Voss, 1992; Peppers & Bradley, 2000). Indeed, *hispidus* as

FIG. 7

Top. *Otodylomys phyllotis* (VB002/MHNG n°1811.090); **middle.** *Peromyscus yucatanicus* (VB225/MHNG n°1812.010); **bottom.** *Sigmodon hispidus* (VB147/MHNG n°1812.004). Dorsal, ventral, and lateral view of cranium and lateral view of left dentary. Scale bars: 5 mm.

currently recognized may prove to consist of several morphologically cryptic but genetically distinct geographical units, and particularly in Central American populations that have virtually received no revisionary attention (Voss, 1992).

Traditionally, the genus *Sigmodon* is divided into two controversial (Elder & Lee, 1985) taxonomic groups: the *S.hispidus* and the *S.fulviventor* groups. Apart from the members of the *S.fulviventor* group from which it differs by having a sparsely haired tail, with large scales (0.75 mm wide rather than 0.5 mm), *S.hispidus* could be confused with the two other species of the *S.hispidus* group: *S.arizonae* and *S.mascotensis*. But, whereas *S.h.* is ubiquitous in Central America – its range extends from Northern Venezuela to Central and South-East United States, but it is absent from the west coast of Mexico – *S.a.* and *S.m.* are confined to the northern and southern part respectively of the Mexican west coast (Zimmerman, 1970). As a result, the three species are not expected to be sympatric in Belize.

S.h., *S.a.*, and *S.m.* are remarkably uniform in external appearance, with virtually no interspecific variation. *S.h.* is, nevertheless, distinguishable by having a generally shorter hind foot – less than 34 mm, usually averaging 32 mm (Cameron & Spencer, 1981; Zimmerman, 1970). With a mean of 26.5 mm, the adult (Voss, 1992) specimens examined during the present study are therefore clearly below the average. Similarly, the external and cranial measurements of VB146 (MHNG n°1812.003), VB147 (MHNG n°1812.004), and VB148 (MHNG n°1812.005) are rather at the bottom (Tables 4, 5), or below, those given for *S.h.* in Cameron & Spencer (1981), Voss (1992), and Goodwin (1969). However, they better correspond to the measurements given in Jones *et al.* (1974) for specimens that were caught to the west of Chetumal, Quintana Roo, Mexico. The latter observations lead to formulate the hypothesis of a morphologically smaller *S.h.* population in the south of Quintana Roo and northern Belize, and further underlines the need for a complete revision of the genus in the Yucatán Peninsula.

Several skull characters allowed VB146, VB147, and VB148, to be identified. Indeed, the combination of a distance between the temporal and occipital ridges inferior to 3.6 mm, a foramen ovale with a diameter inferior to 3/4 the diameter of M3, and a well developed crest on the posterior part of the bony palate distinguish them clearly from *S.a.* and *S.m.* (Zimmerman, 1970). Also, they differ from *S.a.* by having a narrower ventral surface of the presphenoid, a blunt and rather broad spinous anterodorsal process of the zygomatic plate, and an angular supraoccipital crest in posterior view (Severinghaus & Hoffmeister, 1978).

S.h. is a habitat specialist, generally found wherever grass is a significant component of the local vegetation (Voss, 1992). This is confirmed by the fact that specimens of the present study were only captured in vegetation types 6 and 7 of the site n°6 (Tables 1, 2); *S.h.* is therefore expected to be ubiquitous in such habitats, but absent from the forests of SNR. Furthermore, all specimens of *S.h.* were caught on the ground, and ran away on the ground when released. Besides, no morphological adaptations towards arboreality were observed from sampled specimens, thus confirming that *S.h.* is strongly terrestrial.

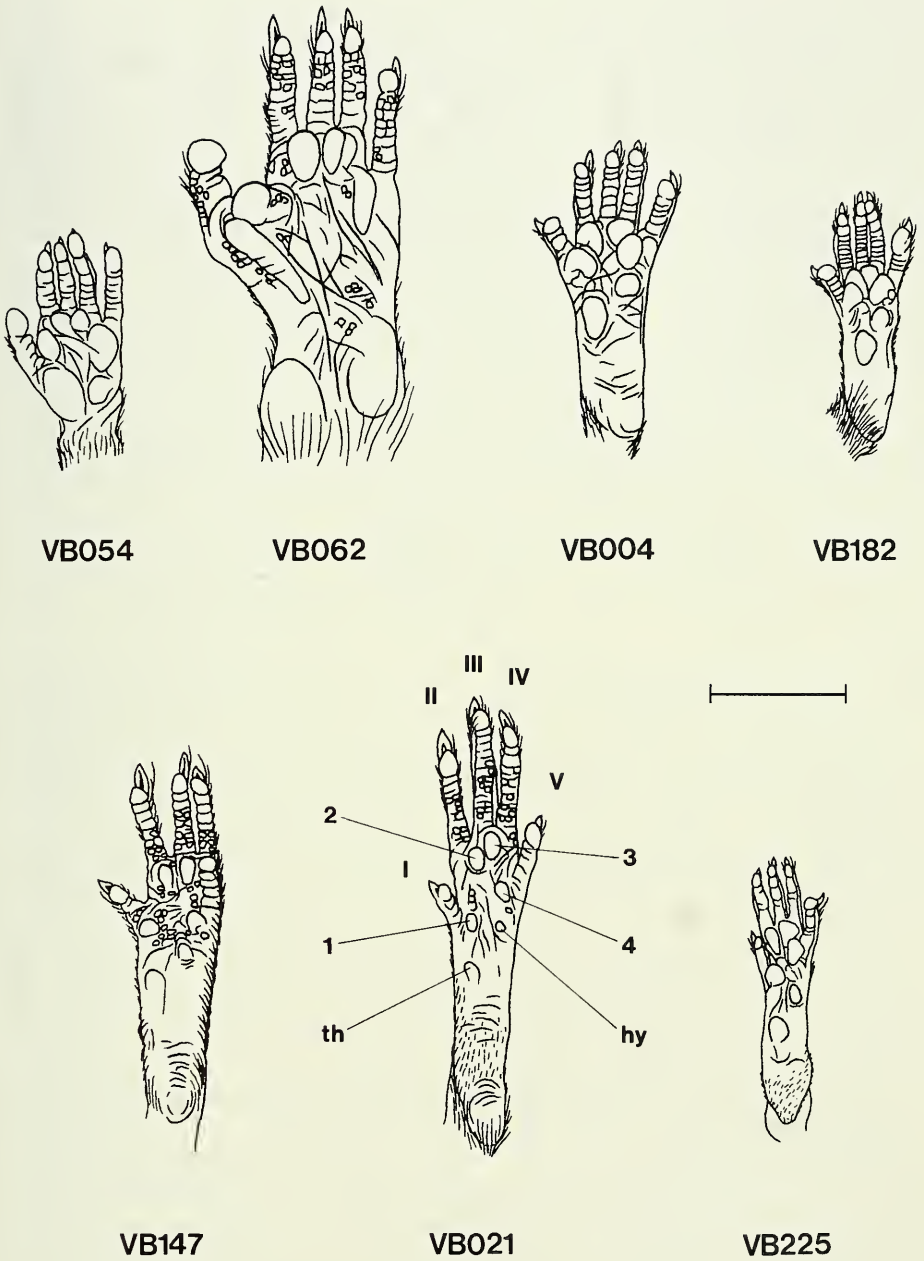


FIG. 8

Marmosa mexicana (VB054), *Didelphis virginiana* (VB062), *Heteromys gaumeri* (VB021), *Otonyctomys hatti* (VB182), *Otodylomys phyllotis* (VB004), *Peromyscus yucatanicus* (VB225), and *Sigmodon hispidus* (VB147). Plantar view of left pes. **hy**, hypothenar pad; **th**, thenar pad; **1-4**, carpal pads; **I-V**, digits. Scale bar: 10 mm.

GENERAL DISCUSSION

Ideally, fieldwork should be continued until asymptotic species lists are obtained. This is nearly achieved in the case of several Central American field stations with long histories of inventory work, where high diversity – quantified as species richness (number of species) – was obtained (Voss & Emmons, 1996); but even in these regions, new species were recently added to the overall list. In the vicinity of the La Selva Biological Station, nearby the Braulio Carrillo National Park, Costa Rica, up to 114 mammalian species including 5 species of marsupials and 13 species of small rodents were recorded since the first inventory published by Slud in 1960 (Timm *et al.*, 1989). Further south in central Panama, up to 113 mammalian species including 6 species of marsupials and 10 species of small rodents were obtained from Barro Colorado Island, Gatun Lake, since Enders' surveys from 1929 to 1937 (Eisenberg & Thorington, 1973; Voss & Emmons, 1996). In the states of Veracruz and Oaxaca, Mexico, two species accounts based on long-term studies were reported by Hall & Dalquest (1963), and Goodwin (1969) respectively. In the first case, 156 mammalian species including 4 species of marsupials, 48 species of small rodents, and 7 species of shrews were recorded since Dalquest's first account in 1947. And in the state of Oaxaca, 204 mammalian species including 6 species of marsupials, 54 species of small rodents, and 10 species of shrews were listed since McDougall's surveys from 1943 to 1967.

By comparing the present study with the latter inventories, the list of small mammals obtained in Shipstern Nature Reserve appears very incomplete with only 2 species of marsupials, and 5 species of myomorph rodents. However, an expedition of six months is considered as very brief, and in such a case adding missing species to the inventory is just a matter of time. An essential problem with inventory comparisons is highlighted by the latter remark. Indeed, all inventory methods are biased because each is suitable for collecting or observing only a fraction of the morphologically and behaviorally diverse mammalian fauna that inhabits Neotropical forests, and special methods are required to add elusive species to faunal lists (Voss & Emmons, 1996). Hence, many methods must be used in combination to census whole communities, and virtually all existing inventories are incomplete. Furthermore, the degree of incompleteness is inversely correlated with inventory duration, so that species lists always increase with additional sampling effort up to an asymptote.

Consequently, results obtained in the present study are better compared to other short term inventories. In Belize, Rabinowitz & Nottingham (1989) sampled small mammals in the Cockscomb Basin of the Maya Mountains for several months in 1983 and 1984. Inventory sites such as the latter comprising both riparian and terra firme habitats are likely to have more diverse mammalian communities than more arid sites such as the one in SNR. This was confirmed by their results, with 4 species of marsupials, including *M.mexicana*, and 9 species of myomorph rodents, including *O.phyllotis* and *S.hispidus*. Besides, they recorded that three species – *Heteromys desmarestianus*, *Tylomys nudicaudus*, and *O.phyllotis* – accounted for 67.5% of the total capture. With *O.phyllotis* accounting for 90.8% and *H.gaumeri* 5.55% of the total capture (Table 1), results are even more striking in SNR, and confirm the general trend

highlighted by Fleming (1975) that neotropical mammal communities generally contain one or two relatively common species and many uncommon species of small mammals. Similarly, Disney (1968) reported from his study in central Belize that *O.phyllotis* and *H.gaumeri* were together the most common species with 76.7% of the total capture. Perhaps, these two species are the most aggressive of the community in northern Belize, and preclude the capture of trap-shy species.

Recently, another study was completed in the Chiquibul Forest Reserve of the Maya mountains (Caro *et al.*, 2001). Their capture results were fairly similar to those of Rabinowitz & Nottingham (1989), with 4 species of marsupials including *M.mexicana* and *D.virginiana*, and 7 species of myomorph rodents, including *H.gaumeri* and *O.phyllotis*. By combining these latter results with those obtained in SNR, it appears that at least 4 small mammal species – *M.mexicana*, *D.virginiana*, *H.gaumeri* and *O.phyllotis* – are sympatric throughout Belize. In addition, two species of squirrels – *Sciurus yucatanensis* and *S.deppei* – were recorded from the Cockscomb Basin, Chiquibul Forest Reserve, and SNR by sight (Appendix III), and can also be considered as sympatric. However, a main difference in SNR is the presence of species such as *O.hatti* and *P.yucatanicus* that are endemic to the Yucatán Peninsula (McCarthy *et al.*, 1998). In this way, with additional endemics such as *H.gaumeri* and *S.yucatanensis*, the small mammal fauna in SNR appears to be closely related to the rodent fauna listed by Jones *et al.* (1974) in Yucatán.

The overall trapping success (3.5%) realized in this study falls within the range of observed success rates in other neotropical small mammal inventories. In the state of Minas Gerais, Brazil, Da Fonseca & Kierulff (1989) recorded a trapping success of 2.4%, and Stallings (1989) 7.5%. In the Maya Mountains, Belize, Rabinowitz & Nottingham (1989) recorded a trapping success of 5.23%, and Caro *et al.* (2001) 0.8%. However, the site-to-site trapping success realized in Shipstern Nature Reserve (Table 3) is fluctuating markedly, ranging from 1.2% in site n°2 to 8.8% in site n°4. Such a fluctuation was also reported by Stallings (1989) where the trapping success ranged from 2.3% to 18.8% from one site to another. In the case of SNR, these irregular trapping results are unlikely to be due to a temporal fluctuation in density, since both sites n°2 and 4 were surveyed during the driest months. Furthermore, the highest results (8.8% and 6.6%) were both recorded from sites n°4 and 8, that is in the Shipstern area (Fig. 2). The latter observation leads to consider a possible higher density in forests situated south to Shipstern Lagoon, at least for *O.phyllotis*. Indeed, such results are biased by the very high predominance of *O.phyllotis* in sites n°4 and 8 – with a total capture of 96.5% and a recapture rate of 2.3, and 95.2% and 1.8, respectively (Table 1) – and therefore cannot be extrapolated to other species such as *H.gaumeri* which remained fairly elusive with a recapture rate of 1.0.

The results of this small mammal inventory give substance to the impression of a diverse rodent community that is clearly affiliated to the partly endemic fauna of the Yucatán Peninsula, Mexico. Besides, they demonstrate the important role that *O.phyllotis* plays in the community structure of small mammals in SNR. That a single species of rodent represents such a high percentage of the total capture, was not recorded in any of the studies cited in the text. Thus, the trapping methods used during this inventory may prove to be particularly effective in trapping *O.phyllotis*, but this factor alone

is surely not preponderant. Consequently, further study focused on the ecological requirements of this species will be of great interest with a view to characterizing the overall ecosystem prevailing in SNR. On the other hand, much research at the community level will be needed to ascertain the role of *O. phyllotis*, and other small mammals, in their maintenance of predators at higher trophic levels. Finally, by referring to the very short period in which the collecting took place, and the small mammal species list predicted from range overlap in appendix II, the sympatric diversity concretely obtained in SNR is certainly underestimated. In this way, further sampling will be needed to assess the presence of other small mammal species in the reserve, and the present inventory is therefore regarded as a preliminary assessment.

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APPENDIX I: Tables 1-6

TABLE 1. Capture results. Field numbers in brackets correspond to the specimens captured at each site. See text for discussion.

Site n°1 (VB001-VB016) 18°18'493"N / 88°11'182"W					
Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Ototylomys phyllotis</i>	27	100.0	16	100.0	1.7
Total :	27	100.0	16	100.0	-
Site n°2 (VB017-VB031) 18°18'119"N / 88°12'679"W					
Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Heteromys gaumeri</i>	6	31.6	4	26.7	1.5
<i>Ototylomys phyllotis</i>	13	68.4	11	73.3	1.2
Total :	19	100.0	15	100.0	-
Site n°3 (VB032-VB058) 18°15'004"N / 88°15'002"W					
Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Marmosa mexicana</i>	1	2.1	1	3.7	1.0
<i>Heteromys gaumeri</i>	2	4.2	1	3.7	2.0
<i>Ototylomys phyllotis</i>	44	93.7	25	92.6	1.8
Total :	47	100.0	27	100.0	-
Site n°4 (VB059-VB123) 18°11'890"N / 88°11'209"W					
Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Didelphis virginiana</i>	1	0.7	1	1.5	1.0
<i>Heteromys gaumeri</i>	3	2.1	3	4.6	1.0
<i>Ototylomys phyllotis</i>	136	96.5	60	92.4	2.3
<i>Peromyscus yucatanicus</i>	1	0.7	1	1.5	1.0
Total :	141	100.0	65	100.0	-
Site n°5 (VB124-VB144) 18°17'567"N / 88°12'912"W					
Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Heteromys gaumeri</i>	7	19.4	6	28.6	1.2
<i>Ototylomys phyllotis</i>	29	80.6	15	71.4	1.9
Total :	36	100.0	21	100.0	-

Site n°6 (VB145-VB172) 18°18'159"N / 88°12'046"W

Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Heteromys gaumeri</i>	3	6.1	3	10.7	1.0
<i>Ototylomys phyllotis</i>	36	73.5	18	64.3	2.0
<i>Sigmodon hispidus</i>	10	20.4	7	25.0	1.4
Total :	49	100.0	28	100.0	-

Site n°7 (VB173-VB207) 18°15'760"N / 88°15'998"W

Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Heteromys gaumeri</i>	1	1.9	1	2.9	1.0
<i>Otonyctomys hatti</i>	1	1.9	1	2.9	1.0
<i>Ototylomys phyllotis</i>	51	96.2	33	94.2	1.5
Total :	53	100.0	35	100.0	-

Site n°8 (VB208-VB231) 18°13'638"N / 88°10'879"W

Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Heteromys gaumeri</i>	1	2.4	1	4.2	1.0
<i>Ototylomys phyllotis</i>	40	95.2	22	91.6	1.8
<i>Peromyscus yucatanicus</i>	1	2.4	1	4.2	1.0
Total :	42	100.0	24	100.0	-

Sites n°1-8

Species	Total captures	% Total	First captures	% Total	Recapture index
<i>Marmosa mexicana</i>	1	0.25	1	0.45	1.0
<i>Didelphis virginiana</i>	1	0.25	1	0.45	1.0
<i>Heteromys gaumeri</i>	23	5.55	19	8.15	1.2
<i>Otonyctomys hatti</i>	1	0.25	1	0.45	1.0
<i>Ototylomys phyllotis</i>	376	90.8	200	86.6	1.8
<i>Peromyscus yucatanicus</i>	2	0.5	2	0.9	1.0
<i>Sigmodon hispidus</i>	10	2.4	7	3.0	1.4
Total :	414	100.0	231	100.0	-

TABLE 2. Capture results per vegetation type. Vegetation types, see table 6.

Sites n°1-8		Vegetation types										
Species	Total captures	1	2	3	4			5	6	7	8	
				P	L	Pu	Ti	Mu	Ta			
<i>Marmosa mexicana</i>	1	1	-	-	-	-	-	-	-	-	-	-
<i>Didelphis virginiana</i>	1	-	-	-	-	-	-	-	1	-	-	-
<i>Heteromys gaumeri</i>	23	6	7	3	-	-	-	-	6	-	-	1
<i>Otonyctomys hatti</i>	1	1	-	-	-	-	-	-	-	-	-	-
<i>Ototylomys phyllotis</i>	376	233	24	27	7	-	-	33	12	6	3	31
<i>Peromyscus yucatanicus</i>	2	1	-	-	-	-	-	-	-	-	-	1
<i>Sigmodon hispidus</i>	10	-	-	-	-	-	-	-	-	-	9	1
Total :	414	242	31	30	7	-	-	33	19	6	12	33

TABLE 3. Trapping success. See text for discussion.

Site n°	Trapping periods	No. trap nights	No. captures	% success
1	May 1-11	1600	27	1.7
2	May 19-29	1600	19	1.2
3	June 6-16	1600	47	2.9
4	June 21- July 1	1600	141	8.8
5	July 11-21	1600	36	2.3
6	Aug 28-Sept 7	1600	49	3.1
7	Sept 11-21	1600	53	3.3
8	Sept 26-30	640	42	6.6
Total :		11840	414	3.5

TABLE 4. External measurements. Body (mm) and mass (g) measurements are presented for adults of both sexes. n, sample size. Other abbreviations, mean and standard error, are defined in text.

Variable	Mean (n=1)			
	<i>M.mexicana</i>	<i>D.virginiana</i>	<i>O. hatti</i>	<i>P. yucatanicus</i>
TL	323	389	199	191
TV	174	186	108	92
HF	20	33	19	22
E	22	35	13	19
NEB	35	58	26	28
NEC	16	26	13	15
SR	35	-	22	26
Weight	66	170	24	24

Variable	<i>Heteromys gaumeri</i>			<i>Ototylomys phyllotis</i>		
	Mean ± SE	Range	n	Mean ± SE	Range	n
TL	266.6 ± 5.58	252-286	5	263.87 ± 1.64	227-295	91
TV	138.4 ± 3.98	128-147	5	123.76 ± 1.09	97-150	94
HF	31.13 ± 0.9	25-33	8	23.55 ± 0.1	21-29	95
E	16.88 ± 0.3	16-18	8	22.2 ± 0.12	19-26	92
NEB	33.13 ± 0.3	32-34	8	35.9 ± 0.19	29-41	93
NEC	18.88 ± 0.77	17-24	8	17.05 ± 0.14	11-20	93
SR	9.4 ± 0.24	9-10	5	7.83 ± 0.09	6-10	94
Weight	60.22 ± 3.54	50-75	9	65.46 ± 1.15	43-96	102

Variable	<i>Sigmodon hispidus</i>		
	Mean ± SE	Range	n
TL	236.2 ± 6.3	220-253	5
TV	97.2 ± 1.93	94-104	5
HF	26.5 ± 0.62	24-28	6
E	17.8 ± 0.58	16-19	5
NEB	34.0 ± 1.03	31-37	6
NEC	16.17 ± 0.7	14-18	6
SR	15.0 ± 0.0	15-15	5
Weight	84.67 ± 3.68	70-92	6

TABLE 5. Cranial measurements (mm), presented for adults of both sexes. n, sample size. Other abbreviations, mean and standard error, are defined in text.

Variable	Mean (n=1)		Variable	Mean (n=1)	
	<i>M.mexicana</i>	<i>D.virginiana</i>		<i>M.mexicana</i>	<i>D.virginiana</i>
ONL	35.41	56.99	MB	12.68	18.77
CBL	34.42	55.6	OCB	7.11	12.42
NL	15.27	26.24	BB	12.65	19.21
BN	4.71	8.85	ZB	20.02	29.4
PL	18.96	34.24	IB	6.1	11.33
PW	9.53	17.91	IOC2	5.97	9.39
PPL	13.41	16.77	CD	11.43	16.66
RL	12.05	23.19	C-M4	13.38	20.03
RW	5.59	11.57	M1-M4	6.38	12.96
BRJ	10.38	16.06	CLMT	3.29	14.36
BRF	6.65	9.91	LM	24.8	42.31
BOL	4.68	5.92			

Variable	<i>Heteromys gaumeri</i>			Mean (n=1)	
	Mean ± SE	Range	n	<i>O. hatti</i>	<i>P. yucatanicus</i>
ONL	35.46 ± 0.25	34.97-35.75	3	28.67	28.8
CBL	33.27 ± 0.19	32.95-33.62	3	25.77	26.86
CIL	29.49 ± 0.1	29.34-29.67	3	24.81	25.49
NL	14.44 ± 0.34	13.85-15.01	3	9.21	11.09

PL	20.28 ± 0.45	19.44-21.0	3	12.4	14.42
PPL	10.51 ± 0.23	10.12-10.93	3	11.11	10.56
LD	9.22 ± 0.36	8.51-9.63	3	6.75	7.98
RL	15.56 ± 0.18	15.27-15.88	3	9.63	11.1
BR	6.33 ± 0.23	6.07-6.79	3	4.79	5.05
LIF	2.87 ± 0.24	2.62-3.34	3	4.75	5.86
BIF	0.91 ± 0.04	0.84-0.96	3	2.38	2.49
BZP	4.36 ± 0.06	4.29-4.49	3	1.46	2.04
OL	8.81 ± 0.05	8.71-8.89	3	8.76	8.92
LBP	8.0 ± 0.25	7.57-8.42	3	3.88	4.09
BBP	5.34 ± 0.11	5.2-5.56	3	4.95	5.18
MPFL	4.33 ± 0.17	4.06-4.64	3	5.03	4.88
MPFW	2.12 ± 0.12	1.98-2.35	3	2.11	1.75
BOL	4.95 ± 0.1	4.79-5.14	3	4.51	3.78
BL	4.87 ± 0.07	4.75-5.0	3	7.84	4.19
BW	3.54 ± 0.08	3.45-3.69	3	5.54	3.38
MB	14.81 ± 0.27	14.43-15.32	3	12.79	11.55
OCB	6.88 ± 0.22	6.45-7.21	3	6.15	6.53
LB	13.52 ± 0.33	13.13-14.17	3	10.66	11.59
BB	13.51 ± 0.17	13.3-13.85	3	13.1	11.87
ZB	16.41 ± 0.15	16.19-16.7	3	14.29	13.04
IB	8.82 ± 0.06	8.7-8.88	3	4.79	4.67
CD	11.56 ± 0.15	11.32-11.84	3	11.58	9.55
BM1	1.35 ± 0.05	1.3-1.45	3	1.28	1.28
CLM1-3	4.6 ± 0.19	4.32-4.97	3	3.99	4.22
DI	1.45 ± 0.05	1.37-1.55	3	1.33	1.37
HI	5.29 ± 0.15	5.06-5.57	3	3.57	3.64
CLMT	4.79 ± 0.06	4.66-4.87	3	4.16	4.29
LM	15.01 ± 0.14	14.79-15.28	3	13.22	14.31

*Ototylomys phyllotis**Sigmodon hispidus*

Variable	<i>Ototylomys phyllotis</i>			<i>Sigmodon hispidus</i>		
	Mean ± SE	Range	n	Mean ± SE	Range	n
ONL	36.81 ± 0.61	33.86-38.86	8	32.82 ± 0.78	31.59-34.26	3
CBL	34.37 ± 0.67	30.94-36.84	8	30.94 ± 0.74	29.64-32.19	3
CIL	32.08 ± 0.55	29.43-34.18	8	30.55 ± 0.68	29.3-31.65	3
NL	12.48 ± 0.29	11.55-13.65	8	11.81 ± 0.37	11.07-12.25	3
PL	18.15 ± 0.32	16.44-19.05	8	17.34 ± 0.43	16.56-18.05	3
PPL	13.74 ± 0.36	12.27-15.42	8	11.39 ± 0.34	10.82-11.98	3
LD	9.02 ± 0.14	8.42-9.55	8	9.19 ± 0.36	8.49-9.64	3
RL	12.96 ± 0.31	11.73-13.93	8	11.81 ± 0.46	10.9-12.32	3
BR	5.87 ± 0.12	5.36-6.26	8	6.53 ± 0.2	6.21-6.9	3
LIF	7.15 ± 0.12	6.4-7.55	8	7.75 ± 0.19	7.41-8.05	3
BIF	3.28 ± 0.09	2.97-3.68	8	2.44 ± 0.14	2.21-2.69	3
BZP	2.93 ± 0.09	2.69-3.46	8	3.03 ± 0.1	2.86-3.22	3
OL	10.79 ± 0.11	10.33-11.13	8	10.44 ± 0.33	10.1-11.11	3
LBP	4.62 ± 0.07	4.29-4.82	8	5.87 ± 0.11	5.76-6.08	3
BBP	6.2 ± 0.11	5.84-6.67	8	6.67 ± 0.29	6.14-7.15	3
MPFL	6.3 ± 0.2	5.65-7.37	8	4.66 ± 0.26	4.4-5.18	3
MPFW	2.47 ± 0.04	2.29-2.58	8	2.07 ± 0.13	1.82-2.26	3
BOL	5.16 ± 0.14	4.6-5.89	8	5.06 ± 0.1	4.94-5.27	3
BL	6.33 ± 0.09	5.81-6.64	8	5.86 ± 0.07	5.73-5.95	3
BW	4.47 ± 0.12	4.04-4.98	8	4.16 ± 0.01	4.14-4.18	3
MB	13.54 ± 0.14	12.82-14.05	8	12.61 ± 0.31	12.1-13.16	3
OCB	7.51 ± 0.14	6.83-7.93	8	6.7 ± 0.16	6.44-7.0	3

LB	11.93 ± 0.24	10.76-12.83	8	11.89 ± 0.44	11.25-12.73	3
BB	14.33 ± 0.18	13.49-15.13	8	13.14 ± 0.2	12.86-13.53	3
ZB	17.82 ± 0.28	16.7-18.78	8	18.11 ± 0.59	16.96-18.87	3
IB	5.84 ± 0.16	5.13-6.67	8	4.88 ± 0.11	4.72-5.09	3
CD	11.44 ± 0.07	11.22-11.85	8	12.16 ± 0.25	11.65-12.43	3
BM1	1.67 ± 0.01	1.61-1.71	8	1.74 ± 0.04	1.68-1.81	3
CLM1-3	6.0 ± 0.06	5.68-6.15	8	5.08 ± 0.07	4.99-5.23	3
DI	1.65 ± 0.05	1.4-1.81	8	1.89 ± 0.02	1.86-1.92	3
HI	3.79 ± 0.16	3.11-4.46	8	5.73 ± 0.14	5.48-5.95	3
CLMT	5.96 ± 0.05	5.72-6.08	7	5.89 ± 0.17	5.64-6.21	3
LM	17.77 ± 0.3	16.73-18.77	7	17.22 ± 0.65	16.03-18.26	3

TABLE 6. Vegetation types 1 to 8. The New Trail, Main Trail, Xo-Pol, and Shipstern areas correspond to trapping sites 1/6, 2/5, 3/7, and 4/8 respectively (Fig. 2).

Vegetation type	n°	Description
Yucatecan medium-sized semi-evergreen forest	1	This forest type (30-50 ft) covers most of the land situated to the west of the reserve, including the Xo-Pol area, as well as the land situated to the south of Shipstern Lagoon, including the Shipstern area. But, whereas it alternates with extensive Cohune forests in the latter, such is not the case in the Xo-Pol area where Cohune trees are virtually absent. Dominant species composing its canopy are: <i>Brosimum alicastrum</i> , <i>Hampea trilobata</i> , <i>Coccoloba reflexiflora</i> , <i>Bursera simaruba</i> , <i>Metopium brownei</i> , and <i>Manilkara zapota</i> (emergent tree). Dominant understory species are: <i>Pithecellobium stevensonii</i> , <i>Coccoloba schiedeana</i> , <i>Ouratea lucens</i> , <i>Randia aculeata</i> , and <i>Croton reflexifolius</i> . Beside <i>Brosimum alicastrum</i> , differential species for this vegetation type are: <i>Dendropanax arboreus</i> , <i>Nectandra salicifolia</i> , <i>Pouteria campechiana</i> , <i>Protium copal</i> , <i>Quararibea funebris</i> , <i>Sabal yapa</i> , <i>Swarzizia cubensis</i> , <i>Tetrapteris schiedeana</i> , <i>Talisia olivaeformis</i> , and <i>Nectandra coriacea</i> . An additional differential species, <i>Cryosophila stauacantha</i> , is found in the Xo-Pol area.
Yucatecan medium-sized semi-deciduous forest	2	This forest type (30-45 ft) covers part of the land situated north of the reserve, where it alternates with Low semi-deciduous <i>Pseudophoenix s.sargentii</i> forests. In the Main Trail area, it is transitioning to vegetation type 1. Dominant species composing its canopy and its understory are similar to the Yucatecan medium-sized semi-evergreen forests, therefore it is very difficult to differentiate between the two. Besides, no differential species for it have been clearly brought out yet. Hence, it is mainly characterized by the absence of species such as <i>Brosimum alicastrum</i> , or <i>Pseudophoenix s.sargentii</i> that are distinguishing vegetation types 1 and 3 respectively.
Low semi-deciduous <i>Pseudophoenix s.sargentii</i> forest	3	This forest type (20-40 ft) covers part of the land situated north of the reserve, including the New Trail area, where it alternates with Yucatecan medium-sized semi-deciduous forests. Some patches of it – coinciding with previously disturbed areas, after the passage of hurricane Janet in 1955 – are dominated by <i>Lysiloma latisiliquum</i> , and can be considered as a structural variant called <i>Lysiloma</i> -dominated <i>Pseudophoenix s.sargentii</i> forest. In the latter, the canopy is almost exclusively composed of <i>L.latisiliquum</i> , which will be gradually replaced by the usual canopy species yet confined to the understory. Otherwise, dominant species composing its canopy and its understory are fairly the same as in vegetation types 1 and 2, with commonly

associated species such as *Agave augustifolia* and *Diphysa carthag-nensis*. Differential species from this forest type are: *Pseudophoenix s.sargentii*, *Ceiba aesculifolia*, *Coccothrinax argentata*, *Erythroxylum rotundifolium*, *Gymnopodium floribundum*, *Hintonia octomera*, *Lysiloma latisiliquum*, *Neomillspaughia emarginata*, *Plumeria obtusa*, *Eugenia buxifolia*, *Randia truncata*, and *Beaucarnea ameliae*.

- Low periodically inundated forest 4 This heterogeneous type of low forest (10-20 ft) is represented by four closely related vegetation types called Pucteal, Tintal, Mucal and Tasistal. Often growing in a complicated mosaic, locally called “Bajo forest”, these plant communities are patchily scattered all over the reserve, and only part of them have yet been localized. Whereas the elevation and duration of inundation are gradually decreasing from the Mucal to the Pucteal, the Tasistal forms an open habitat (Tasiste marsh) close to being permanently inundated. It is dominated and differentiated by the palm *Accoelorrhapha wrightii*, which is typically found with *Erythroxylum areolatum*, *Eugenia acapulcensis*, and *Jacquinia aurantiaca*, along with occasional species such as *Crescentia cujete*, *Borreria verticillata*, *Enstonia exaltatum*, and *Cladium jamaicense*. The Mucal forms a shrub forest (Muc marsh) dominated by *Dalbergia glabra*, which is typically found with species such as *Cameraria latifolia* and *Malpighia lundellii*. The Tintal forms a semi-open habitat (Tinta marsh) dominated by *Haematoxylon campechianum* and *Byrsonima bucidaefolia*. The Pucteal forms a low forest dominated by *Bucida buceras*.
- Bravaisia tubiflora*-dominated transitional zone 5 This type of low forest (10-25 ft) is mainly found in the surroundings of Shipstern Lagoon, where true forest is transitioning to open wetlands – in most cases, *Cladium jamaicense*-dominated herbaceous wetlands. Such transitional zones are inundated at the peak of the rainy season, whereas their soils remain water-saturated for most of the year. However, it can also be present in forest areas bordering more permanent bodies of water. It is dominated and differentiated by *Bravaisia tubiflora*, which is typically found with *Croton reflexifolius*, *Sabal yapa*, *Metopium brownei*, *Eugenia rhombea*, and *Eugenia acapulcensis*, along with occasional species such as *Oncratea nitida*, *Cameraria latifolia*, and *Dalbergia glabra*.
- Cladium jamaicense*-dominated herbaceous wetlands 6 This type of wetland (3-5 ft) is found in the surroundings of Shipstern Lagoon, where it forms a transitional belt between true forest and mangal flats. Often preceded by a *Bravaisia tubiflora*-dominated transitional zone, the belt varies in width from nearly nothing to about 350 ft (100m). It is dominated and differentiated by *Cladium jamaicense*, which is normally found with species such as *Conocarpus erectus* and *Solanum blodgettii*. Assimilated to this vegetation type, an omnipresent variant dominated by *Distichlis spicata* forms another transitional belt between the *Cladium jamaicense*-dominated belt and the mangal flats.
- Discontinuous dwarf mangal interrupted by bare salt flats 7 This type of mangal association (3-6 ft) covers most of the periodically inundated surface bordering Shipstern Lagoon, and extending to areas of transition with true forest. Also found along the coast, it represents the dominant vegetation type within the reserve. It is fairly intermittent, with large patches of ground being completely bare of vegetation, sometimes interrupted by so-called “forest islands” – punctual change in ecological conditions allowing various vegetation types to establish, including *Thrinax radiata*-dominated low forests (not considered as a distinct vegetation type). It is dominated by the red mangrove (*Rhizophora mangle*), which constitutes well-developed

communities along the lagoon, but is otherwise found in patches of its dwarf counterpart. Typical associated species are the white (*Laguncularia racemosa*) and the black (*Avicennia germinans*) mangroves, only found in dwarf form. Occasionally, species such as *Distichlis spicata*, *Fimbristylis spadicea*, *Batis maritima*, and *Salicornia perennis* are also found in this vegetation type.

- Cohune forest 8 With the exception of a few small patches localized in the Xo-Pol area, this forest type (50-70 ft) is exclusively found in the deep soils of the land situated south of the lagoon, including the Shipstern area. It alternates with Yucatecan medium-sized semi-evergreen forests, and patches of Low periodically inundated forests. The dominant and differential species composing the canopy is the cohune palm: *Orbignya cohune*. Associated canopy and understory species are otherwise similar to vegetation type 1.

APPENDIX II: Sympatric diversity in SNR

This appendix presents a diversity estimate for the small mammal fauna of Shipstern Nature Reserve. The following list does not include the sampled and sighted species :

Gray Four-eyed Opossum	<i>Philander opossum</i>
Central American Woolly Opossum	<i>Caluromys derbianus</i>
Robinson's Mouse Opossum	<i>Marmosa robinsoni</i>
Hispid Pocket Gopher	<i>Orthogeomys hispidus</i>
Forest Spiny Pocket Mouse	<i>Heteromys desmarestianus</i>
Coue's Rice Rat	<i>Oryzomys couesi</i>
Rusty Rice Rat	<i>Oryzomys rostratus</i>
Northern Pygmy Rice Rat	<i>Oligoryzomys fulvescens</i>
Northern Climbing Rat	<i>Tylomys nudicaudus</i>
Slender Harvest Mouse	<i>Reithrodontomys gracilis</i>
Maya Small-eared Shrew	<i>Cryptotis mayensis</i>

This small mammal species list was predicted from range overlap – geographic expectations (Voss & Emmons, 1996) – and is mainly based on distributional data obtained from Reid (1997), Emmons & Feer (1997), and McCarthy *et al.* (1998). The known ecological requirements for each species was also taken into account, so as to minimize inaccuracy in diversity estimate. Thus, the Water Opossum (*Chironectes minimus*) is probably not present in the Shipstern Nature Reserve – it is semi-aquatic, favoring fast-flowing, rock- or gravel-bottomed streams in hilly country (Reid, 1997) – although its range is seemingly overlapping the area. Inversely, *Marmosa robinsoni* is presently considered as absent from northern Belize, but as already discussed, a reappraisal of all specimens of the species in Central America is needed to determine its exact distribution, so that it may well be present throughout Central America. Being a habitat generalist, *M. robinsoni* would therefore be expected in SNR. In the case of the Maya Small-eared Shrew (*Cryptotis mayensis*), information on its known geographic and ecological distribution is complemented by the observation of a non-identified species of shrew in the vicinity of SNR (Walker, 2000; pers. obs.).

By combining the present list (11 species) with the 7 sampled species of marsupials and myomorph rodents, and 3 sighted species of marsupial and squirrels – *Didelphis marsupialis*, *Sciurus yucatanensis*, and *S. deppei* – a total of 21 small mammal species is expected in SNR. This diversity estimate, however, is subject to several sources of uncertainty, and is to be considered as a first approximation.

APPENDIX III : Observed mammals in SNR

This appendix presents an inventory of the mammalian species observed during the field-work in Shipstern Nature Reserve. The observations were primarily based on direct sightings

(D), but also on indirect indices – nests (N), sets of tracks (T), scats (Sc), and sounds (So). A total of 19 small, medium-sized, and large mammals was thus obtained from SNR and its direct surroundings. In the following list, the numbers are related to the areas – New Trail (1), Main Trail (2), Xo-Pol (3), and Shipstern (4) areas (Fig. 2) – from which the corresponding species were recorded :

Common Opossum	<i>Didelphis marsupialis</i>	D/So	3
Northern Tamandua	<i>Tamandua mexicana</i>	D/So	4
Nine-banded Armadillo	<i>Dasybus novemcinctus</i>	D	2
Yucatán Squirrel	<i>Sciurus yucatanensis</i>	D	3
Deppe's Squirrel	<i>Sciurus deppei</i>	D	3
Mexican Porcupine	<i>Coendou mexicanus</i>	D	1
Central American Agouti	<i>Dasyprocta punctata</i>	D	1,2,4
Paca	<i>Agouti paca</i>	D/So	1
Gray Fox	<i>Urocyon cinereoargenteus</i>	D/So	1,2,3
White-nosed Coati	<i>Nasua narica</i>	D/N	1,3,4
Kinkajou	<i>Potos flavus</i>	D	4
Tayra	<i>Eira barbara</i>	D	3
Puma	<i>Puma concolor</i>	T	3
Jaguar	<i>Panthera onca</i>	T/Sc/So	2,3
Ocelot	<i>Leopardus pardalis</i>	T/So	4
Collared Peccary	<i>Tayassu tajacu</i>	D/So	1
Baird's Tapir	<i>Tapirus bairdii</i>	T	2,3
Red Brocket	<i>Mazama americana</i>	D/T/So	3
White-tailed Deer	<i>Odocoileus virginianus</i>	D/T/So	3